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Reviews

Ontogenetic development and evolution of the worker caste in termites

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Summary. The hemimetabolous termites have a very different caste system from social Hymenoptera in which only true imagoes participate in all social tasks. In termites, the imagoes are restricted to reproduction. The termite solidiers have no equivalent in other social insects. They are unique both in their post-embryonic development and their exclusively defensive function. At maturity they keep their molting gland and therefore should be considered as stabilized, differentiated immatures. They appeared monophyletically, early in the evolution of termites.

The definition of the worker caste and the current theories explaining its evolution are reexamined after a critical reappraisal of data on post-embryonic development. On the basis of ontogenic, morphologic and functional criteria, we define termite workers as individuals diverging early and irreversibly from the imaginal development, with a morphology typical of their caste but largely of larval appearance, and taking part in most of the social tasks.

Such a truly eusocial worker caste is observed in all advanced phyla: Termitidae, Hodotermitidae, and *Schedorhinotermes* (Rhinotermitidae), but apparently also in one morphologically primitive termite, *Mastotermes darwiniensis*. This distribution can only be explained by postulating a polyphyletic origin of the worker caste in termites. In all other primitive termites, most of the work is done by temporary helpers (late larvae and nymphs). In these societies, pseudergates are redefined as individuals separating late from the imaginal line, functioning as workers, but not constituting the main working force in the natural society.

The particularity of the caste system in termites results from two fundamental peculiarities of their post-embryonic development:

- A certain dissociation of molt, growth, and differentiation.
- A relative independence in the ontogeny of their different organs.

Key words. Social insects; Isoptera; caste differentiation; reproductive biology; evolution.

Introduction

In eusocial insects, division of labor or polyethism is often linked to polymorphism, i.e. morphologically distinct individuals or castes perform different tasks. Caste differentiation is a developmental process. By comparison to non-social insects, 'normal development' leads to fertile, winged imagoes, i.e. the sexual caste. The development of neuters diverges from this at a more or less definite stage, the 'decision point' sensu Oster and Wilson[51], which occurs during post-embryonic or sometimes embryonic development. The neuters must therefore be considered as the product of deviations from the normal development leading to the imagoes. This simple idea has too often been overlooked in the study of polymorphism[12].

In the Hymenoptera, there are two fundamental castes, the queens and the workers, the latter being polymorphic in some cases. Morphological differences between the two castes are more or less important, and it seems that the earlier the differentiation the greater are the differences. Queens and workers, however, are imagoes. Their differentiation ends at the imaginal molt which definitively stabilizes their morphology. The immature stages, larvae and pupae, are entirely dependent on the workers and are incapable of participating actively in social tasks.

The situation is completely different in the termites. Being hemimetabolous insects, they can be active participants in the society's tasks well before the imaginal molt. In termite societies, the only imagoes are the alates, which after swarming become the primary reproductives, kings and queens.

Termite soldiers cannot be considered as a subcaste of workers as in some ants where the 'soldiers' are simply major workers whose particular morphology can be explained by an often small modification of their allometric growth. The development of a termite soldier has no equivalent in other insects[10]. Even if their development ends at this stage, they cannot be considered as true imagoes for the very simple reason that their prothoracic glands do not degenerate during morphogenesis. Despite their great morphological diversity, all termite soldiers share the same unique development, passing through a characteristic pre-soldier or white soldier stage. It thus appears that the differentiation of the soldier caste has been a monophyletic event which occurred very early in the evolutionary history of the Isoptera.

Termite workers are far less easy to recognize morphologically than the soldiers, especially in some primitive families, and no unique developmental pathway can define them. Workers are not imagoes, and that is one of the main reasons why this caste is so difficult to define. Until recently, most authors considered 'true workers' as only being present in higher termites, but that individuals called 'pseudergates' may represent an early attempt towards worker differentiation in primitive families[35,39,44,47,70]. Recent studies, however, by Watson and co-workers, have led to a completely different interpretation[68,69]. As a result, there is presently not only a divergence of view concerning the evolution of polymorphism in termites, but also a great confusion in the very definition of the worker caste and in the concept of the pseudergate, in both their meaning and utility.

The confusion is such that a reassessment of termite polymorphism seems necessary. In the present paper, we will review the current theories on the origin of termite polymorphism. After a critical review of the data on which these theories were based, we will attempt a new synthesis, including new definitions of the controversial terms.

Current theories on the origin of the worker caste

For a long time, a distinction was made between the 'higher termites' (Termitidae), in which a worker caste is always very distinct, and 'lower termites' (essentially Kalotermitidae and Termopsidae sensu Grassé[15]), which are without workers. In the latter, worker functions are carried out by older larvae (apterous) and nymphs (immatures with wing buds), i.e. by individuals in various stages of imaginal development (reviewed in Light[28]).

With increasing knowledge of the termite developmental pathways, this simplistic picture has become more elaborate. Grassé and Noirot[19] found evidence of *regressive* and *stationary* molts in *Kalotermes flavicollis* which introduced an unsuspected flexibility into its development (see below). Regressive and stationary molts deviate the individuals from the normal, imaginal development into *pseudergates*. These observations were confirmed and extended by Lüscher[32] who proposed, however, a developmental sequence which suggested that a pseudergate stage is an obligatory step in the development of imagoes (compare figs 1 and 2).

It was also demonstrated that the workers of the Termitidae, which are clearly defined both morphologically and functionally, are not in the great majority of cases in a terminal stage. They remain capable of further development by molting, either in other worker stages, or in soldiers or even in sexual ergatoids[44].

Finally, Buchli[7] found a developmental pathway in the genus *Reticulitermes* (Rhinotermitidae) which appeared as intermediate between those of higher and lower termites, this being consistent with the family's taxonomical position. Buchli reported both the existence of workers much alike those of the Termitidae and a developmental flexibility as great as that in *K. flavicollis*. Under experimental conditions at least, regressive molts producing individuals equivalent to the pseudergates were demonstrated.

From these studies, and from less detailed observations on other lower termites, a concept of worker caste evolution has emerged which can be summarized as follows:

In primitive eusocial termites (a soldier caste is already present), post-embryonic development was linear as in the non-social Orthopteroids. The worker functions were simply carried out by older larvae or nymphs. Next the potential of stationary and regressive molts permitted certain individuals (pseudergates) to deviate from the 'normal' path by remaining for extended periods in a functional worker phase without losing their other ontogenetic potentialities. In the course of evolution, this deviation made by the pseudergates from the imaginal development occurred earlier and earlier during the ontogenesis of the insects. Finally a branched developmental pathway evolved as observed in the present Termitidae. Post-embryonic development splits very early on into a 'normal line', leading to the imagoes, and a neuter line. This ontogenetic divergence is accompanied by an increasingly marked division of labor within the societies. Pre-imaginal stages no longer participate in the society's tasks and become completely dependent on the workers.

This evolutionary schema was expounded several times by one of the present authors[44,46,47] and seemed generally accepted[70]. It was, however, recently challenged by Watson and Sewell[68,69] on the basis of new observations made by Watson et al.[67] on *Mastotermes darwiniensis* and by Sewell and Watson[63] on several Australian *Kalotermes* in which they claim to recognize a worker caste. These authors have formulated a theory completely opposite to the one just described. The early separation during development of an imaginal and a neuter line would be a primitive condition. The polymorphism of *Kalotermes flavicollis*, far from being considered as primitive, is now interpreted as a secondary adaptation to an unstable environment. Since the worker caste would thus be present at the origin of all present termites, the concept of a pseudergate (representing a proto-worker in some of them) becomes obsolete and must be discarded.

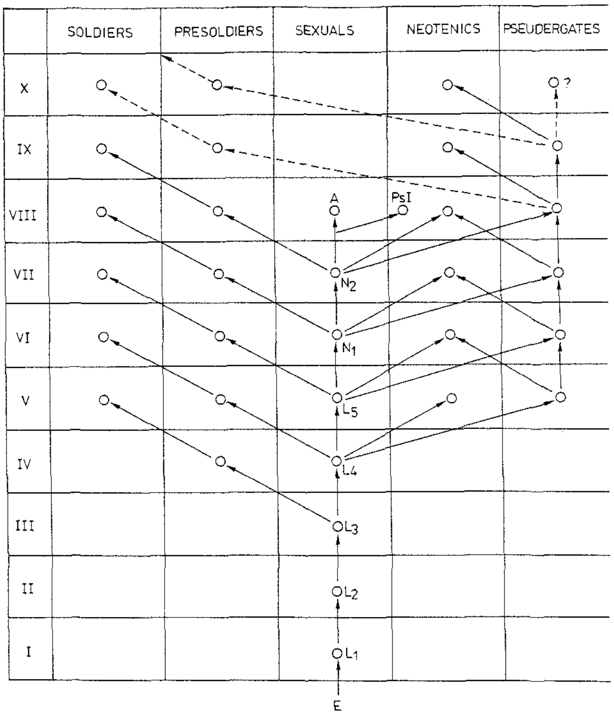

Figure 1. Developmental pathway of *Kalotermes flavicollis* according to Grassé and Noirot. The *normal* developmental line ends in imaginal alates (A), but many *deviations* may occur. The pseudergates differ either from larvae (stadium IV) in an ascending way, or nymph (stadium V–VII) in a descending way (regressive molt). (From Grassé and Noirot, 1947, slightly modified). E: egg; L1–L5: larvae; N1–N2: nymphs; PSI: pseudimago. Since the original study of Grassé and Noirot, three nymphal stages have been recognized in *K. flavicollis*[49].

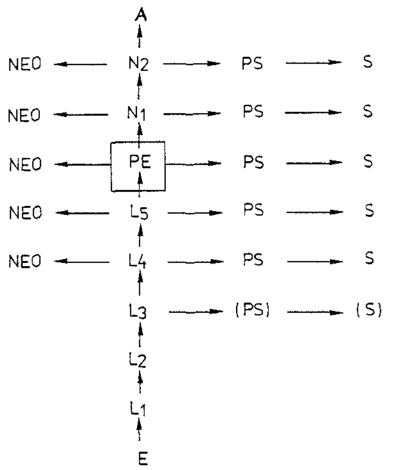

Figure 2. Developmental pathway of *Kalotermes flavicollis* according to Lüscher. In this schema, the pseudergate (PE) seems to be an *obligatory* intermediate in the development of the imaginal alates (A). Otherwise, the development of neotenic reproductives (NEO), presoldiers (PS) and soldiers (S) follows the same way as in fig. 1. (Redrawn from Lüscher[31]).

Watson and Sewell's interpretations seem unacceptable to us, but the discussion of their observations and conclusions must also include a re-examination of previous theories and concepts.

At the center of the debate is the very definition of the termite worker. To clearly understand what a termite worker is, one must first examine the most highly evolved species, the Termitidae, in which workers are always present and recognizable without ambiguity. Having identified the distinctive characteristics of this caste, we will try to unravel the issue in the lower termites, and will re-examine the definition and significance of the pseudergates.

The workers of Termitidae (higher termites)

A worker is an individual who works. No simple truism, this definition is particularly well adapted to the Termitidae workers, which have as their exclusive prerogative all the main social tasks (food gathering, nest construction, feeding the brood, sexuals and soldiers) with the exception of reproduction, carried out by the sexuals, and defense, where soldiers play the principal role.

Some nuances must of course be brought to this assertion. For example, during the first period of young colonies, the founding pair fulfills these social functions. Soldiers of *Nasutitermes costalis,* even if they do not collect food, recruit workers to new food sources[65,66]. In some primitive genera *(Amitermes, Termes),* older nymphs which sometimes leave the nest may perhaps participate in food collection, though at best marginally.

The worker morphology and anatomy are markedly simplified compared to those of the winged imagoes: absence of wings, reduction of the pterothorax, absence of eyes, reduction of the optic lobes, rudimentary sex organs. They also possess some more distinctive characteristics: development of the head and mandibular muscles, development of the digestive tube. In all, they do not appear to be very specialized, and differences between species are more apparent in terms of behavior than in morphology[48].

The workers' ontogenetic development permits us to perceive the profound differences that separate them from the winged imagoes. If all newly hatched larvae appear morphologically the same, the first molt gives rise to two categories of individuals, which diverge radically in development: the *nymphs,* recognizable by their little wing buds and very small head, and the *larvae,* without wing buds and having a larger head. The first category, destined to become the winged imagoes, already exhibit an important development of the genital organs, and the beginnings of the differentiation of the eyes and optic lobes.

In the second group, however, the development of these structures is arrested. These larvae are therefore morphologically very similar to workers, but differ in the total absence of pigmentation and sclerotization, and especially in their behavior and physiology. The larvae, nearly motionless, cannot leave the nest and are completely dependent on the workers which give them an exclusively liquid diet (most probably a salivary gland secretion). The molt that transforms the larva into a worker is thus devoid of any great structural changes, but instead results in radical changes in physiology and behavior.

The worker in this form is not an imago. In many species, it remains capable of molting, without notable modification, into an advanced worker stage, or, with further differentiation, into a soldier. In fact, the majority of soldiers come from workers in the Termitidae. Even in species where the worker appears unable to molt (e.g. major workers of the Macrotermitinae) their molting glands are still present, albeit appearing inactive.

The workers' post-embryonic development is thus characterized by the cessation of differentiation in a number of organs (pterothorax, genital organs, eyes, and the optic lobes of the brain) which gives them a larval-type morphology. The positive-adaptive changes in the development of the head, digestive tube, and salivary glands are mainly quantitative. The molt which transforms the larva in a functional worker is most certainly followed by extreme changes in physiology and behavior, though with only minor structural modifications. When the workers pass through several successive stages, the only changes that occur are increases, often quite weak ones, in pigmentation and sclerotization of the integument. More rarely, some allometric growth has been reported in the appendages (*Trinervitermes*[44]), or sternal gland (*Nasutitermes*[52], and *Trinervitermes*[27]).

This is why it seems legitimate to us to qualify the molts that mark the development of workers as *stationary molts,* i.e. molts which insure the eventual growth of the insect without notable structural modification. In some ways it is the kind of molt observed during larval life in holometabolous insects, but not, to our knowledge, in other hemimetabolous insects (except perhaps in some Homoptera) where during larval molts, a progressive differentiation of wing buds, flight muscles, sex organs, compound eyes, and optic lobes always occurs.

The stoppage of differentiation, which so profoundly marks the Termitidae workers is not strictly irreversible. The development of workers into neotenic reproductives remains a possibility in a certain number of species where workers can become (generally after two, but sometimes after three, special molts) sexually functional *ergatoids*[45,50,60]. Moreover, these sexual ergatoids sometimes exhibit rudimentary imaginal characteristics such as compound eyes, and expansions of meso- and metathorax suggesting a start in the development of wing buds[50,60,64]. In *Nasutitermes princeps,* various degrees of sexualization have been reported in workers after the elimination of the functional sexuals. Some workers gave rise after several molts to intercastes showing various combinations of worker – soldier – nymph characteristics without, however, becoming functional reproductives[59]. Finally, soldiers of *Nasutitermes lujae* have recently been described which have developed wing buds ('nymphs-soldiers'), but originated from small workers as do normal soldiers[26].

The development of nymphs, ending in winged imagoes, is also subject to perturbations. The development of neotenics from one of the several nymphal stages is known to occur in numerous species, but has rarely been analyzed. The morphology of the neotenics is never absolutely identical to that of normal nymphs. Sexual development requires at least one special molt. A nymphal type of morphology remains, however; if the sex organs develop, the somatic characters do not. The wing buds may even undergo regression. The neotenic molt appears in certain ways as *stationary* or even *regressive* molt. Very recently, true *regressive molts* have been observed in a colony of *N. columbicus* (Noirot and Thorne, in preparation) and in *N. novarumhebridarum*[60], which produced individuals intermediate between nymphs and workers. Although only observed twice, it has revealed in an advanced Termitidae genus a flexibility in the nymphal development that was unsuspected until now.

However, these reversions have been observed only under exceptional circumstances, and they were only partial changes. The differentiation into two lines, imaginal and neuter, already apparent after the first molt, is largely irreversible: a worker cannot become a winged imago, and a nymph cannot develop into a worker or a normal soldier.

Thus, in the Termitidae, the workers are defined by three sets of characteristics: functional, morphological, and ontogenetic. For this last set, the important point is the very early and irreversible divergence of workers from the imaginal line. Workers are usually sterile. Only in some species few workers may become fertile after the lost of the sexuals. They thus represent a truly eusocial caste. In different species however, workers show various ontogenetic potentialities which possibly represent steps in the progressive stabilization of this caste.

The Kalotermitidae

a) *The European Kalotermes flavicollis*

The post-embryonic development of this species, which has been the subject of numerous studies[17–19, 31–33, 35], is characterized by an extraordinary flexibility which renders it very difficult to study. It is, however, possible to define 'normal' imaginal development as consisting of 7 stages, ending with winged imagoes[19]. Wing buds become visible only after the fourth molt; the first 4 stages are thus designated as larval and the following 3 as nymphal[49]. The larvae of the first two stages are completely dependent on their siblings; the third stage larvae already feed themselves[2], but they do not begin to play an effective role in the work of the society until the fourth stage. These stage 4 larvae as well as stages 5 and 6 nymphs, behave as workers; final 7th stage nymphs appear less active, but there is no doubt that they continue to participate in the social tasks[3].

This development may undergo numerous *deviations*. All nymphal stages and 4th stage larvae (even those of 3rd and 2nd stages in very young colonies) may develop into soldiers. All stages from the 4th larval stage (3rd in very young colonies) are able to develop into sexual neotenics. These transformations are irreversible.

A third type of deviation, less obvious and potentially reversible, results from *stationary* and *regressive molts* leading to the pseudergates. The term pseudergate has been used in such a variety of senses that it would appear beneficial to recall the original definition of Grassé and Noirot[19]. They created the term to designate individuals of large size, but with very short wing buds or none at all, a feature which distinguishes them from nymphs of the same size. These pseudergates develop along an *ascending path* where the larvae undergo one or more stationary molts marked by some growth, but without wing bud development. They develop along a *descending reverse path* where the nymphs undergo a regressive molt accompanied by weak growth or none at all, but causing a regression or even a loss of wing buds. We have reproduced here (fig. 1) the developmental schema originally proposed by Grassé and Noirot, which unequivocally illustrates how the pseudergates arise from *deviations* from the normal development. Morphologically, these pseudergates only differ from nymphs by the reduction or absence of wing buds: the other structures, most notably the genital organs, do not appear modified. Subsequent research, particularly that of Lüscher[32], has further specified the remarkable ontogenic potentialities of these pseudergates, which are able to differentiate into soldiers or sexual neotenics, to revert to the nymphal state, or, finally, to remain as pseudergates while undergoing stationary molts. These pseudergates participate in the social tasks, but are apparently no more active than older larvae or nymphs.

The work of Lüscher[31, 32, 34, 35] has modified, to some degree, the image of pseudergates, less by the observations made (which essentially confirm the others), than by his graphic representation of the developmental schema which became a classic (fig. 2). Lüscher's schema suggests that the pseudergate stage is an *obligatory* intermediate in the development of the winged imagoes. Thus, a '*linear*' schema was proposed instead of the '*ramified*' schema of Grassé and Noirot.

The existence of stationary and regressive molts, and the complex steps in post-embryonic development were established principally by studies of termites reared in the laboratory. The research of Lüscher however clearly demonstrates that stationary and especially regressive molts are particularly frequent in small populations (some tens of individuals), like those of most laboratory rearings. More recent observations of molts occurring in natural populations (adult colonies with more than several hundred individuals) have shown that the pseudergate stage is not obligatory[49]. The high frequency of progressive molts (66.5% progressive molts, 27% stationary molts, 6.5% regressive molts; N = 453) showed that a part (undoubtedly important) of the individuals reached the imaginal stage without deviating from the normal 7 developmental steps. These results suggest that in adult colonies pseudergates are far from representing a majority of active individuals and that perhaps their importance in the working of the colony, while not negligible, has been overestimated. This question requires new research.

b) *The Australian Kalotermes*

The detailed observations made by Sewell and Watson[63] led them to propose, for several Australian species of *Kalotermes*, developmental schemata radically different from those describing the development in *K. flavicollis*. It is essential to analyze their observations and conclusions because it is from these that Watson and Sewell[68, 69] construct their hypothesis concerning the evolution of polymorphism in termites.

The Australian authors attach a great deal of importance to the existence of a 'forked developmental pathway': after the *first molt*, the development bifurcates into a 'worker line' without wing buds and an 'alate line' with wing buds. However, in the two cases in which a forked pathway is postulated (*K. aemulus* and a highland form of *K. rufinotum*), this molt was not directly observed and was only deduced from the examination of a very small number of individuals (4 'first stage workers' in *K. aemulus*, 2 'first stage nymphs' in *K. rufinotum*). In both cases, the 2 'lines' rejoin: the so-called workers in the worker line develop into nymphs. In our opinion, this 'forked pathway' does not exist. The presence or absence of tiny wing buds at the second stage is simply an expression of developmental variability, a characteristic trait of the genus *Kalotermes*. Furthermore, other Australian *Kalotermes* studied by Sewell and Watson[63] did not show this 'forked pathway' (*K. rufinotum*, coastal form, *K. banksiae*, *K. atratus*, *K. convexus*, see also Watson and Sewell[68], p. 111).

The other observations made by Sewell and Watson fit well with those already known for *K. flavicollis*, but they are presented with a different terminology and by a peculiar graphic representation of the sequence of molts. The representation is based in fact on one postulate: the existence of 'three developmental lines, an apterous worker line, an alate line, and a reversionary nymphal line' (Watson and Sewell[68], p. 106). In their schemata the three 'lines' are represented as distinct vertical columns (fig. 3). But in all the species studied, the 'alate line' started from the 'worker line', and the 'worker line' always ended in the 'alate line'. Therefore, in all these schemata, imaginal development always follows a zigzag course arbitrarily represented by 3 parallel columns. The schema of a bifurcated development, a neuter and an imaginal line, is simply an artifact of drawing. This concept is obviously closely tied to a definition of workers that must be critically examined. According to Sewell and Watson[63] (p. 245) a worker is 'a primary apterous stage with pigmented gut; such individuals always function as workers'. These criteria cannot define a functional worker because of trophallactic exchanges: in *K. flavicollis*, the larvae 2, which are incapable of feeding themselves, have nevertheless wood in the digestive tube and a complete intestinal fauna. Even in first stage larvae, the digestive tube contains bits of wood and some of the symbiotic flagellates (Grassé and Noirot[16]). In another section Sewell and Watson[63] recognize (p. 245) that 'other stages, including brachypterous and secondarily apterous individuals, may also undertake household chores, so that they, too, are workers, functionally if not developmentally'. The term pseudergate was criticized by Watson et al.[67] (p. 41) because 'it involves two unrelated concepts: a concept of function and a concept of developmental status'. The Australian authors fall into exactly the same trap. They state 'we therefore use the term 'worker' when we refer to the working stages'. (Watson and Sewell[68], p. 104). However in their analyses of the developmental pathways in the Australian Kalotermitidae, Sewell and Watson[63] utilize an *ontogenetic* definition of workers which excludes the majority of 'working stages'. In the Australian *Kalotermes,* as in *K. flavicollis,* the 'worker force' is composed of all the individuals that have attained a sufficient size (probably after the third molt). The ontogenetic definition of Sewell and Watson includes ineffective individuals from very young stages, but excludes nymphs and the 'reversionary line', both certainly more important in the society's activities. Their morphological definition of workers relies solely on the absence of wing buds and the presence of a pigmented gut. Finally their definition leads to circular reasoning. In effect the larvae 2 of other authors are by definition workers. By definition, then, the workers appear early in the course of development. Watson and his co-workers give little weight to the fact that these 'workers' necessarily develop into nymphs! When the functional, morphological, and ontogenetic criteria are applied, the 'worker' caste as defined by Sewell and Watson for the *Kalotermes* is not equivalent to the one found in the Termitidae.

The reversionary line of Watson and Sewell formed by nymphs undergoing one or more *regressive molts* and capable of further stationary molts, is strictly comparable to the pseudergates formed by a descending path in *K. flavicollis.* Even a return to the nymphal state was observed in the highland form of *K. rufinotum.* Thus the Australian species of *Kalotermes* studied by Sewell and Watson appear quite comparable to *K. flavicollis.* The principal variations result from the more or less early appearance of wing buds and, as a consequence, the varying number of 'nymphal' stages preceding the imago. By adopting another mode of representation a schema is easily obtained that is very close to that given by Grassé and Noirot for *K. flavicollis.* This is what we have done in figure 4 for *K. banksiae* where the original schema of Sewell and Watson (fig. 3) has been redrawn using the same mode of representation that was used for figure 1.

c) *Other Kalotermitidae*

Pseudergates (in the original sense of the term) appear present in all the *Kalotermes* studied. Unquestionable examples have also been found in the genus *Neotermes* (*N. jouteli*[43], *N. connexus*[42]), but the detailed study of Kalshoven[24] showed no equivalent form in *N. tectonae,* in which he observed a simple development in 7 stages, without regressive or stationary molts. Pseudergates are equally present in *Pterotermes occidentis*[23] and Zimmerman[72] demonstrated the occurrence of regressive molts in this species. None of these studies contain information about the importance of pseudergates in natural populations, and about their frequency as a function of the age of the colonies, the season etc. However, the information that is available seems to exclude the possibility that they are the only 'functional workers', and indicates that a significant part of the social tasks are accomplished by the older larvae and nymphs.

Family Termopsidae (sensu Grassé, 1949)

The genus *Zootermopsis,* the most often studied, seems comparable to *K. flavicollis.* Individuals, which resemble pseudergates in their large size and absence of wing buds are frequent[8,21,35] and Heath[21] and Sharon Greenberg (pers. comm.) have confirmed the existence of stationary and regressive molts.

Pseudergates also appear to be present in *Archotermopsis*[22], *Stolotermes*[41], and *Porotermes*[37], but regressive molts were apparently not directly observed.

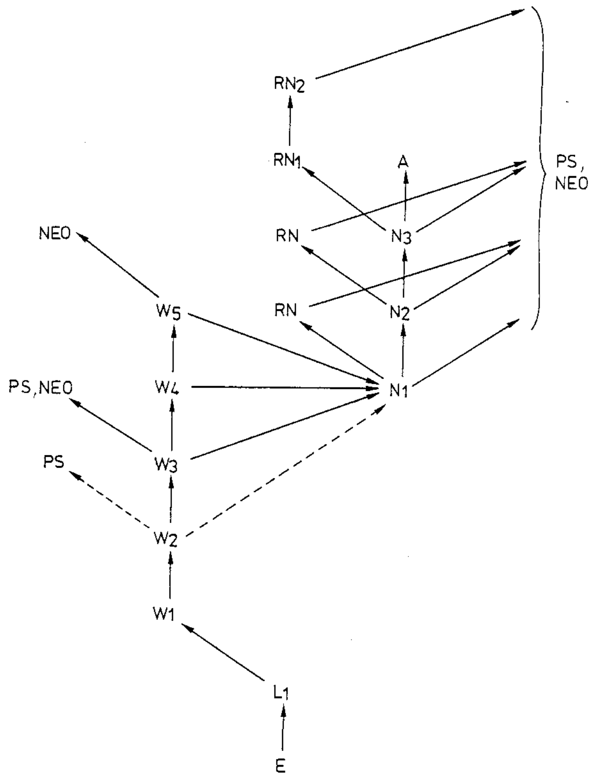

Figure 3. Developmental pathway of *Kalotermes banksiae* according to Watson and Sewell. The 'worker line' (W1–W5) ends in the 'imaginal line' (nymphs: N1–N3 and alates: A). The nymphs may undergo regressive molts to the 'reversionary line' (RN). Presoldiers (PS) and neotenics (NEO) may differentiate from most of the stadia of the 'worker line', the 'nymphal line' and the 'reversionary line'. (From Watson and Sewell, 1981).

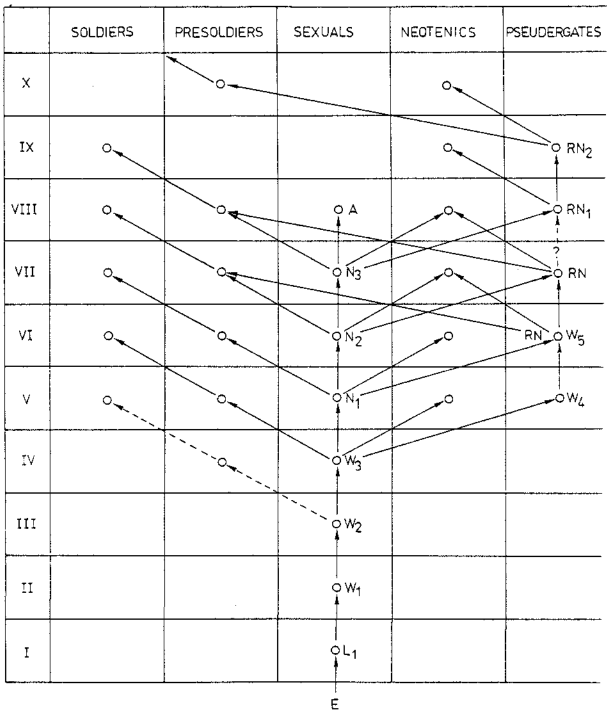

Figure 4. Developmental pathway of *Kalotermes banksiae.* Data of fig. 3 redrawn with the same graphic representation as in fig. 1: the similarity with *K. flavicollis* now becomes evident.

Family Rhinotermitidae

It is of special interest to consider this family because it occupies a transitional position between the 'lower termites' and the Termitidae, and it is believed that the Rhinotermitidae and Termitidae belong to the same evolutionary line[13,25]. In *Prorhinotermes simplex,* Miller[38] showed that the nymphs differentiated quite late, but that they could undergo a regressive molt which gave individuals with a worker-like appearance. These are the equivalent of the pseudergates defined in the Kalotermitidae.

Miller's conclusions were confirmed recently by Roisin[56] working on *P. inopinatus.* In this species also, there is no real worker caste, as defined for the Termitidae. Work is done by late larvae retaining the possibility of alate development. Only one wing-padded nymphal instar is observed, but it can arise from at least 3 apterous instars, even in natural colonies. It is thus difficult to define in this species one 'typical' imaginal development. The nymphs can undergo regressive molts giving rise to pseudergates with larval appearance.

Reticulitermes is the genus which has been the most studied, especially the French species, thanks to the detailed work of Buchli[7]. He demonstrated the existence of workers comparable to those in the Termitidae, differentiating after the second larval molt to form a distinct 'neuter' line which also produced soldiers. These workers are morphologically well defined, not only by the total absence of wing buds, but also by a lack of development of the pterothorax, genital organs, eyes, and optic lobes. As in the Termitidae, these organs stop developing after the differentiating molt. In contrast, the head and digestive tube undergo a notable development. However, these morphological characteristics (and notably the reduction of the thorax) are less pronounced than those found in the workers of the Termitidae[48]. Functionally, they assume nearly all the social tasks, even though the 5th and 6th stage nymphs are capable of feeding themselves, at least in the experimental colonies[7]. The separation of the lines, neuter and sexual, after the second molt is normally irreversible, but in experimental conditions partial reversions are observed, demonstrating a great flexibility in post-embryonic development. Nymphs in all but the last stage can undergo regressive molts which transform them into individuals morphologically more worker-like, and which correspond to the original definition of pseudergates. These nymphs can also become more or less typical soldiers. Thus, the coexistence of true workers and pseudergates can be observed in these species. Conversely, the different worker stages can develop into functional ergatoids, a transformation that requires two successive molts. The intermediate form (observed after the first molt and designated by Buchli as 'pseudonymph'), derived from 4th and 5th stage workers, shows the beginnings of wing bud development, buds which regress more or less completely at the second molt. Thus *Reticulitermes* shows a potential flexibility in post-embryonic development at least equal to that of *Kalotermes* (see fig. 27 in Buchli[7]). But many of the possible variations have only been observed in artificial conditions and have little change of expressing themselves in nature. Pseudergates exist in natural societies, but it is doubtful that they are of any great importance. The essential point, however, is the separation of the two lines, neuter and imaginal, at a definite step, or 'decision point' in post-embryonic development, a separation never completely reversible which permits the recognition of a worker caste in both the morphological and ontogenetic senses of the term. Certainly in this regard, the polymorphism of *Reticulitermes* constitutes an ideal intermediate between *Kalotermes* and the Termitidae.

Roy-Noël[61] observed the splitting in two lines, neuter and alate, after the second molt in *Coptotermes intermedius.* According to a brief note made by Watson and Sewell[68], *Coptotermes lacteus* shows the same separation of imaginal and neuter lines after the second molt, but the possible reversions have not been studied.

In the African species of *Schedorhinotermes,* analyzed by Renoux[54,55], a neuter line also separates itself from the imaginal line at the second molt, but only females undergo this transformation with the result that all the workers and soldiers are female. Regressive molts and pseudergates have never been observed.

Thus the family Rhinotermitidae exhibits a great diversity of developmental patterns, all the more interesting to compare that the examples were taken from different subfamilies and represent as many evolutionary lines:

- Societies apparently devoid of true workers in which polymorphism is more or less comparable to that of the Kalotermitidae and Termopsidae: *Prorhinotermes* (subfamily Prorhinotermitinae sensu Quennedey and Deligne[53]).
- Societies where the neuter and imaginal lines are clearly distinct, but where great developmental flexibility is retained, at least under experimental conditions: *Reticulitermes* (subfamily Heterotermitinae) and perhaps *Coptotermes* (subfamily Coptotermitinae).
- Societies where the two lines are clearly separated and development is extremely rigid, to the point where only one sex produces the neuters: *Schedorhinotermes* (subfamily Rhinotermitinae).

Family Hodotermitidae (Grassé, 1949)

Despite certain morphological resemblances to the Termopsidae, this family has a profoundly different biology and polymorphism, both of which are very close to that of the Termitidae. In *Hodotermes mossambicus*[29,30] a neuter line separates from the normal alate producing line after the second (or perhaps third) molt. A sexual dimorphism in size appears at this time, the males being larger. At the end of the 6th stage, these neuters become functional workers (small female workers, large male workers) but continue to molt with an increase in size and pigmentation. Soldiers differentiate at the end of the last larval stage and in the first worker stage, but only males undergo this transformation. In *Anacanthotermes*[9,36,71] development proceeds as in the preceding case, but the neuter females have disappeared: all the workers and soldiers are males.

Regressive and stationary molts have never been observed and pseudergates do not exist, at least in natural conditions. The workers of Hodotermitidae possess the three groups of characteristics (functional, morphological and ontogenetic) found in the Termitidae workers.

Family Mastotermitidae

The study of *M. darwiniensis,* the only living species in the family, assumes a particular importance because of the primitive character of its morphology. According to Watson et al.[67], Watson and Sewell[69], the development is characterized by a splitting into two lines, worker and nymph, at the first larval molt. This split appears irreversible. In that regard, *Mastotermes* is comparable to the Termitidae. However, a number of peculiarities in development must be noted. The only visible difference after the differential molt is the greater pilosity in the nymphal line compared to the worker line. Curiously this marked pilosity disappears in the last 3 nymphal stages and in the imagoes, albeit reappearing in the neotenics. These neotenics always develop from workers. The nymphs appear to be incapable of such a differentiation. In the nymphal line wing buds appear only in the 4th nymphal stage. In return, the meso- and metanotum of the workers show a lateral expansion reminiscent of wing buds (unpublished observation).

These unique aspects of polymorphism, the presence of chemical defense in the soldiers[40] as well as the occurrence of a type of multiflagellate spermatozoon unique in the animal world[4, 5] and not observed in other termites[6] support the idea that *Mastotermes* belongs to a line apart from the others in the evolution of the termites, and cannot be simply considered, according to its morphology, as a 'primitive termite'.

Peculiarities in the post-embryonic development of termites

Despite certain gaps in our knowledge, we can isolate a number of developmental peculiarities tied to the extraordinary complexity and originality of the termite caste system.

The development of winged imagoes is not different from the development observed in hemimetabolous insects. Wing buds, however, can develop late in some species instead of at birth.

From this imaginal development, deviations can occur at more or less precise stages and in a variety of directions, leading to polymorphism. This extraordinary individual flexibility of development, particular to termites, appears to us to be linked to two fundamental peculiarities of these insects:

- a certain dissociation of molt, growth, and differentiation.
- a relative independance in the ontogeny of the different organs.

These two traits are apparent first in a rather simple way in the stationary and regressive molts observed in the lower termites. During these molts growth is quite variable and may even not occur at all, a halt in the development of some organs is observed as well as a reduction or disappearance of the wing buds during regressive molts.

The development of workers is only an exaggeration of this process. During the differentiating molt that produces the neuter and imaginal lines, larvae which develop into nymphs undergo a normal molt developing genitalia, wing buds, eyes and optic lobes. These organs cease development in those larvae that become workers despite the fact they grow in other important ways. There is little morphological difference between the functional worker and the larvae from which it developed. The additional molts which the workers of many species undergo are essentially stationary molts.

Neoteny, so frequent in the termites and so important in the replacement of the sexuals, illustrates an unusual independence between germinal and somatic development. At least one molt is necessary for the differentiation of these neotenic sexuals. As a result, they are never identical to the larval, nymphal, or worker stages from which they developed. These transformation molts exhibit some unusual characteristics. Gonads and the genital tract obviously undergo an accelerated development, the other imaginal characters developing in a variety of ways. Thus when a neotenic develops from a nymph, there is often a regression of the wing buds or at least a stabilization. However, in neotenics that arise from workers, it is not unusual that small wing buds appear[7, 54, 60, 64]. The compound eyes often show some degree of development and pigmentation occurs; they can even show a clear beginning of differentiation in ergatoid sexuals, but in this case the optic lobes show only insignificant development[60, 64].

The soldiers are the result of an absolutely original morphogenesis, completed in two successive molts, and comparable in certain ways to the metamorphosis of holometabolous insects[10]. During these molts certain organs can regress more or less completely (wing buds in those that arose from nymphs or the digestive tube in certain of the Termitinae[10]), whereas the head is profoundly modified. The nymph-soldier intercastes are clear evidence of the relative independence of the organs during their development. In *Nasutitermes* the intercastes can differentiate from nymphs causing some regression in wing buds, or from workers with the development of wing buds, depending on the species[26].

The worker-soldier-nymph intercastes of *N. princeps*[59] beautifully demonstrate once more the independence between germinal and somatic development as well as the independence of various organs during ontogenesis. All combinations of characteristics of the three castes seem possible.

Finally, a unique example of disconnection between growth and differentiation during imaginal development was recently reported in a Termitidae. Whereas in all species of this family, the alates differentiate from the 5th nymphal stage, in *Nasutitermes princeps* the 4th nymphal stage may also undergo an imaginal molt that results in dwarf alates. Those 'microimagoes' possess otherwise all the characteristics of the ordinary alates and may become functional reproductives, although they cannot fly[57].

How did the caste system evolve in the termites?

The soldier. We have no idea of the first steps in their phylogenetic history since even the most primitive species possess typical soldiers with their characteristic development. There can be little doubt that the soldiers which appeared at the origin of the Isoptera constitute a homologous caste throughout the order. There seems to be a general agreement among social insect experts on this monophyletic origin[70]. But it is also clear that in the beginning soldiers could develop from a variety of developmental stages, consequently a great deal of intraspecific variation in their morphology is observed. All the research on the different species of Kalotermitidae agree in this respect that soldiers develop from nymphs with wing buds as well as from apterous individuals, whether designated as larvae, workers or pseudergates.

When there is an early separation between the neuter and sexual lines, soldiers normally develop from the neuters despite the fact that in *Reticulitermes* it is not exceptional for soldiers to develop from nymphs. Most often, soldiers develop from several worker stages *(Mastotermes, Amitermes ...)*. In most Termitidae soldiers are found to originate from a unique worker stage and from only one sex. The ultimate step in this specialization seems to be reached in the few species where the soldiers are derived from peculiar larvae that are different from worker larvae. Examples can be seen in the small soldiers of *Trinervitermes* and *Acanthotermes*.

It is reasonable to conclude that in the 'Prototermites' the soldier developed from any individual that had attained a sufficient stage. Later, the developmental deviation that produced soldiers became increasingly restricted and in the extreme case resulted in a soldier line separated from the worker line.

The workers. First, it is necessary to return to the definition of a termite worker. The diversity of situations observed in the different groups of termites imposes a certain amount of arbitrariness in this definition. Workers may be defined functionally as individuals that work, or in morphological or ontogenetic terms.

However, it is essential to be consistent, whatever the choice. Watson and Sewell[68] proposed an ethological definition, but then[63] adopted morphological criteria, i.e. the absence of wing buds and a pigmented abdomen. This appears to be an unfortunate choice because it does not correspond to any particular function that the individual performs or to any divergence in development that occurs after some 'decision point'.

The ethological or functional definition is the broadest and appears to us the least informative and even tautological. It simply says that there is a division of labor in these eusocial insects which is only a restatement of the definition of eusociality. In many species, and especially in *Kalotermes*, this leads to calling nearly every member of the society a 'worker' since they participate in social chores. The only exceptions are very young larvae, soldiers, and sexuals. In these societies work is done by temporary helpers.

To avoid this problem we suggest a more restrictive definition. We only recognize the existence of a worker caste, sensu stricto, when tasks are done by morphologically specialized individuals whose development has diverged early and irreversibly from the imaginal line. Workers constitute a sterile, morphologically distinct, eusocial caste. This definition makes use of the three criteria which have already been discussed: functional, morphological and ontogenetic criteria. According to the species, each criterion may be more or less distinct. Workers by our definition constitute the essential worker force of the society even though nymphs may participate to some degree as in *Reticulitermes*. The morphological specialization of the workers is maximal in the Termitidae and Hodotermitidae, clearly less in the Rhinotermitidae and weakest in *Mastotermes*, as can be judged by the development of the pterothorax in *Mastotermes* workers. The ontogenetic potential of the differentiated workers is quite variable from species to species.

From this perspective, is it necessary to keep the concept of pseudergates, and if so, how must they be defined? The original definition given by Grassé and Noirot[19] for *Kalotermes flavicollis* was essentially morphological and ontogenetic: large individuals, similar in size to nymphs, which undergo stationary or regressive molts.

Thus, as do workers, they result from a developmental deviation from the imaginal line. However, this deviation occurs at various stages, late during the post-embryonic development, and not at a 'decision point' that occurs early in development and at a definite step. It must be stressed, that in some species (e.g. *Prorhinotermes inopinatus*[56]) developmental plasticity is such, even in natural societies, that it seems impossible to recognize one 'normal' imaginal line and deviations from it. In such a case, a distinction between a 'normal' or a 'deviate' origin of pseudergates, as illustrated for example by the schema of either Lüscher[31, 34] or Grassé and Noirot[19] for *K. flavicollis*, appears to be a question of taste in our present state of knowledge. Pseudergates retain an extensive developmental potential, but when reversion to imaginal development is possible as in *Kalotermes*, it appears to occur infrequently. Morphologically, the only difference between pseudergates and nymphs lies in the reduction of wing buds without any other change in the thorax. From what we know the sex organs do not appear to change. In morphological and ontogenetic terms their differences with workers s.str. are more quantitative than qualitative. Functionally, pseudergates behave as workers, but the important point for us is that they do not constitute in any case the only, or even the principal 'worker force' of the society, which includes older larvae and nymphs in the Kalotermitidae and Termopsidae or true workers in *Reticulitermes*.

We believe that the term pseudergates fulfills a necessary function, and propose the following definition:

- Individuals that deviate late from the imaginal line, essentially by a regressive molt, and also by stationary molts in species where visible wing buds appear late during the development. In this latter case (pseudergates of the 'ascending path' sensu Grassé and Noirot[19]) 'deviations' from the imaginal line are not always recognizable by straightforward criteria.
- Individuals functioning as workers, but sharing this function with other categories.

The concept of pseudergates is justified not only by considerations discussed below, but because it also emphasizes one of the most remarkable peculiarities of post-embryonic development found in the majority of primitive termites.

How did the worker caste evolve in termites?

So far, those who have studied termite polymorphism (including the senior author of this paper) have admitted implicitly that this caste has a monophyletic origin, or at least that its evolution occurred in a similar way in the different evolutionary lines. The existing species could thus illustrate various steps in a single evolutionary process.

A monophyletic origin is also postulated by Watson and Sewell[68]. They further postulate that a bifurcated developmental pathway, with both neuter and sexual lines, appeared very early on in the history of the Isoptera. The pathway described in *Kalotermes flavicollis* would have evolved as a response to an unstable environment.

We believe we have demonstrated that the developmental pathway of *K. flavicollis* is characteristic of the Kalotermitidae, Termopsidae or certain Rhinotermitidae in which a worker caste equivalent to the one found in higher termites does not exist. It is difficult to imagine repeated losses of the worker caste only in the primitive termites often living in ecological conditions identical to those of the advanced Termitidae. If the selective pressure resulting from an unstable environment was really determining, one should expect that Kalotermitidae living in more stable regions, such as humid tropical or equatorial regions, would have retained the bifurcated pathway and the worker caste. The existing data do not support this view (in particular, Kalshoven[24]). It is interesting to note that the secondary loss of the soldier caste is only observed in some higher Termitidae, never in primitive termites.

It is much simpler to admit that the absence of workers is a primitive trait, often encountered in primitive termites. It follows, however, that *the worker caste has a polyphyletic origin in the Isoptera*. Indeed, the three families of lower termites, Mastotermitidae, Hodotermitidae and Rhinotermitidae, in which a worker caste has been reported, must have diverged before the evolution of this caste. The Mastotermitidae, which is the oldest line, seem to share a common ancestor with the Kalotermitidae. The Hodotermitidae have their origin in the Termopsidae, while the Rhinotermitidae developed from another branch of the Termopsidae[14]. Moreover, in the Rhinotermitidae, the evolution of a worker caste must have occurred after the separation of the family, since workers are not present in *Prorhinotermes* (belonging to the primitive subfamily Prorhinotermitinae recently created by Quennedey and Deligne[53]). Furthermore, the status of workers is quite different in *Reticulitermes* and *Schedorhinotermes* (see above). In higher termites also, the monophyletism of the worker caste may be questioned. The evolution of the Termitidae from a branch of the Rhinotermitidae seems well established[1, 14]. Did this ancestor already possess workers? It is difficult to give a definitive answer. However, one observation goes against this hypothesis. In the subfamily Macrotermitinae, the workers are preceded by three larval stages, but only two in the other subfamilies[44]. There are reasons for thinking that the Macrotermitinae separated early on from the common stem of the Termitidae[20, 62] although Emerson[13] and Krishna[25] do not share this opinion. Recent morphological studies on the epipharynx have led Deligne[11] to suggest a family status for the Macrotermitinae, which would thus be removed from the Termitidae. It could be that the workers developed after the evolution of the Termitidae line, and that they evolved independently once in Macrotermitinae, and once in the other three subfamilies, but this remains speculative.

Thus, the worker caste has appeared several times during the evolution of the Isoptera, and the common characters which occur in the different lines are a result of convergent or parallel evolution: it is parallel evolution if the steps in differentiation are the same, and convergent if they are different from one line to another.

Two evolutionary schemata seem possible. In the first, there is a progressive reduction or regulation in developmental flexibility. Late and reversible deviations first give rise to pseudergates. Little by little these deviations occur earlier and at definite steps. Finally, there is a bifurcation in post-embryonic development that separates the neuter and imaginal lines. In this hypothesis, pseudergates are the ancestors of the true workers, still present today in some primitive groups.

In the second schema, the early differentiation of an irreversible and distinct neuter line is an original phenomenon which appeared later in the evolution but at first was added to (and coexisted with) the flexible primitive form of development, finally replacing it. According to this interpretation, pseudergates are not the workers' ancestors, but are their analogs in the primitive societies with less specialized castes. In the two hypotheses, the pseudergates represent an evolutionary step that preceded the worker caste. In the first, there is a progressive transformation from pseudergate to worker, in the second, a replacement of the pseudergates by the workers. The state of our knowledge does not allow us to make a choice at this moment. An intermediate case such as *Reticulitermes* could be interpreted both ways.

A precise study of the seasonal developmental cycle, and of its determinism, could help to resolve this question. It is possible that in the primitive termites without true workers, the developmental cycle (imaginal molt and swarming) is simply regulated by the seasonal changes in temperature, whereas the appearance of a neutral line programmed early on in the post-embryonic development, occurring at a precise 'decision point', is tied to a more refined seasonal control.

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Amoeboid movement: A review and proposal of a 'membrane ratchet' model

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Summary. Diverse cell types, including Amoebae, leukocytes, embryonic cells and tumour cells move about on solid surfaces to accomplish such activities as feeding, bacterial destruction, embryological development and metastasis. Theories of the mechanism of this movement are reviewed and a model is proposed which invokes the existence of specific, laterally mobile, transmembranous structures in the cell membrane, which are reversibly adhesive for both the contractile apparatus of the cell internally, and the substratum externally. By this model, the movement of all these cell types can be explained.

Key words. Amoeboid movement; Amoebae; polymorphonuclear leukocytes; cells.

Introduction

Amoeboid movement is a motion performed by single cells whilst adherent to solid surfaces and is exhibited by free-living protozoa, especially Amoebae, by leukocytes and to a lesser extent by embryonic cells, tumour cells and metazoan cells in tissue culture. A most satisfying theory of amoeboid movement would be one which could apply to all these cell types. However, despite numerous suggestions in reviews[1–7], monographs[8,9], and symposia[10–16], no such single mechanism has been described.

This paper summarises the phenomena of amoeboid movement and theories of its mechanism, as well as proposing a new model based on reversible adhesive transmembranous structures acting in a manner analagous to a ratchet.