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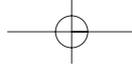


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REVIEW ARTICLE

The life cycle of *Reticulitermes* spp. (Isoptera: Rhinotermitidae): what do we know?

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Abstract

The subterranean termites in the genus *Reticulitermes* have a complex and plastic life cycle, which has been the subject of a number of publications over the past century. Given the inherent difficulties in studying such cryptic, eusocial organisms it is not perhaps surprising that the literature on their biology has failed to reach a consensus. An overview of the literature is given, which is followed by a discussion of the various theories on the life cycle of *Reticulitermes* spp. A substantial proportion of the review focuses on the French literature, which constitutes the majority of the primary sources and can be difficult to access. There are many discrepancies in the literature in terms of the number of instars, the definition of workers and the question of whether they should be termed pseudergates or, potentially, an additional terminology used to differentiate between pseudergates and the true workers seen in the higher termites (Isoptera: Termitidae). It remains very difficult to compare publications as there is little conformity; a problem that is aggravated by a general absence of drawings of the relevant instars. Further work on the biology of *Reticulitermes* is clearly required. There is also a need for researchers to agree on a standard terminology for this genus. A glossary is provided for the various synonyms and definitions.

Introduction

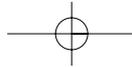
The life cycle of *Reticulitermes* species (Isoptera: Rhinotermitidae) has been the subject of much debate (Grassi & Sandias, 1893; Snyder, 1915; Hare, 1934; Feytaud, 1946; Grassé, 1949; Grassé *et al.*, 1950; Buchli, 1958; Harris & Sands, 1965; Noirot & Pasteels, 1988; Takematsu, 1992; Vieau, 1994a, 1999). This is in part due to the difficulties that arise in studying a subterranean organism. They also have

an extremely plastic biology. Life cycle studies on *Reticulitermes* species have not been conducted for several decades, possibly because it is assumed that sufficient knowledge has already been gained. However, in reviewing the primary literature, most of which is in French (Lespès, 1856; Feytaud, 1946; Grassé, 1949; Grassé *et al.*, 1950; Buchli, 1958; Esenther, 1969; Noirot, 1985; Noirot & Pasteels, 1988), it became apparent that the life cycle is not well understood. There have been recent reviews that have dealt with the genus *Reticulitermes* (Thorne, 1998; Thorne *et al.*, 1999) but these did not go into detail about the problems associated with the various life cycle theories.

The aim of this review is to compare and consolidate the different life cycle pathways proposed to date. Central to the debate is the work of Buchli (1958) which has been the basis

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for most subsequent reviews (Noirot & Pasteels, 1987; Thorne, 1996, 1998). The present review is especially relevant in the light of the finding that the European species *Reticulitermes santonensis* (Feytaud) appears to be synonymous with the North American species *Reticulitermes flavipes* (Kollar) as this makes the (European) literature on *R. santonensis* more widely applicable (Jenkins *et al.*, 2001).

Life history

European termites were initially thought to have the same life cycles as those from the tropics (Thompson, 1917), although not enough is known about each species to support this view and Thorne (1998) stated that species within the genus *Reticulitermes* should not be considered to all have the same life history. However, general comments are still made about the genus as a whole, which makes the review of this topic extremely difficult.

The most recent detailed investigation of the life cycle of the European species, *R. santonensis* and *R. lucifugus* (Rossi) was performed by Buchli (1958). However, some of his methodology was flawed. He performed very few replicates and marked some termites by amputation of a leg, almost certainly affecting their behaviour. Cannibalism of such damaged individuals by other members of the colony would have been likely. Buchli concentrated on the study of *R. santonensis* but could have confused the two species, a serious flaw because *R. santonensis* and *R. lucifugus* appear to have different developmental pathways and reproductive strategies. Both species have the capacity to form secondary reproductives, but dispersion and spread in *R. santonensis* is now thought to be mainly via secondary reproductives while in *R. lucifugus* it is via alates (Vieau, 1999).

Many of the post-embryonic forms described by Buchli (1958) may not exist in the field (Noirot, 1985; Noirot & Pasteels, 1987; Vieau, 1994a,b). The title of Buchli's thesis, 'The ontogenic potential...' even suggests that these were not all naturally occurring individuals. The caste organization described by Buchli (1958) was extremely complex and was later simplified by Noirot (1985). The explanation of neoteny (reproduction via supplementary reproductives), one of the most important developmental paths, was omitted (Noirot, 1985; Vieau, 1996).

The study of post-embryonic development in termites is extremely complex. It can be difficult to count the number of moults, polymorphism can occur, and individuals may show different developmental pathways. Termite social behaviour is also very complex and they have a lengthy developmental time (Weesner, 1965). That any instar can eventually develop into either a primary or secondary reproductive, means that a viable colony could form from any group of individuals (Noirot, 1990). The existence of parthenogenesis in *Reticulitermes* species has had mixed support and has only been seen in a few species (Grassi & Sandias, 1893; Buchli, 1950b; Weesner, 1956; Nutting, 1969; Howard *et al.*, 1981; Pawson & Gold, 1996; Matsuura & Nishida, 2001).

Terminology

Termite colonies are composed of individuals of different castes, which have a similar function in all termites (Noirot, 1985): the alates (primary reproductives), neotenics (replacement or secondary reproductives), nymphs (developing individuals in the sexual line), workers

(individuals in the neutral line), pseudergates, larvae and soldiers. In *Reticulitermes* species, all castes are made up of individuals from both sexes (Pérez, 2007; Snyder, 1926).

The terminology of termite development is a source of much confusion (Forschler & Jenkins, 1999) due to the use of the same terms to describe different stages. This is particularly evident when comparing the older literature (Thompson, 1917; Grassé, 1949; Weesner, 1965; Vieau, 1994a; Thorne, 1996, 1998). For this reason, a glossary is provided at the end of the review for the various synonyms and definitions (appendix 1).

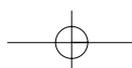
The terminology used in this review is that of Buchli (1958). The numbering of different stages is based on the work of Vieau (1994a, 2001) (fig. 1). The preferred terminology is shown in bold. The term **larva** or white immature is used for the first two stages after hatching (L1 and L2). Two pathways then occur, the worker line (where individuals have no wing buds) (W3 to W7) and the sexual or nymphal line (where individuals have wing buds). Workers can develop either into soldiers, via an intermediary stage called '**white soldiers**', or into secondary reproductives called apterous neotenics and third-form reproductives or **ergatoids**, which have no wing buds (Weesner, 1965; Krishna, 1989; Thorne, 1996, 1998). The nymphal line is made up of four initial nymphal stages (N3 to N6). After the N6 stage there is a split in a line where individuals can either develop into **nymphs with long wing buds** (LWBN) or nymphs with short wing buds, referred to as a **pre-neotenic brachypterous stage** (PBNEO) (Vieau, 1994a, 2001). The LWBN will go on to develop into an **alate**, also called an imago, (termed primary or first-form reproductive once they have lost their wings). Nymphs with short wing buds (PBNEO) will develop into **brachypterous neotenics** (BNEO), also referred to as second-form reproductives (secondary reproductives with wing buds) (Weesner, 1965; Krishna, 1989; Thorne, 1996, 1998; Vieau, 2001). The three adult forms were defined by Thompson (1917). Although the first form and brachypterous neotenics were originally described by Lespès (1856), whose terminology was taken up by Grassi & Sandias (1893), the term 'secondary reproductive' refers to any reproductive apart from the primary reproductive (i.e. alates that have lost their wings) that founded the colony. In contrast, the term 'supplementary reproductive' is given to secondary reproductives that develop whilst the primary pair are still alive (Thorne, 1996).

Instar differentiation

Termite instars can be separated by the width of the head capsule (Hare, 1934; Buchli, 1958; Clément, 1979). Measurements of antennae and wing pads have also been used (Hare, 1934; Buchli, 1958). Individuals preparing to moult stop eating, almost completely empty their stomachs and become milky in appearance (Grassé, 1949; Buchli, 1958). The exuviae are either eaten by the individual itself or by other larvae or workers (Grassé, 1949).

Egg to L2

In *Reticulitermes* species, eggs are laid approximately 15 days after mating and eggs in a colony are generally found in clumps of 500–1000 (Feytaud, 1946; Grassé, 1949; Vieau, 1991, 1996). Lespès (1856) reported that in *R. lucifugus*, eggs are found in clumps of about 100 but the age of the colonies





Reticulitermes life cycle

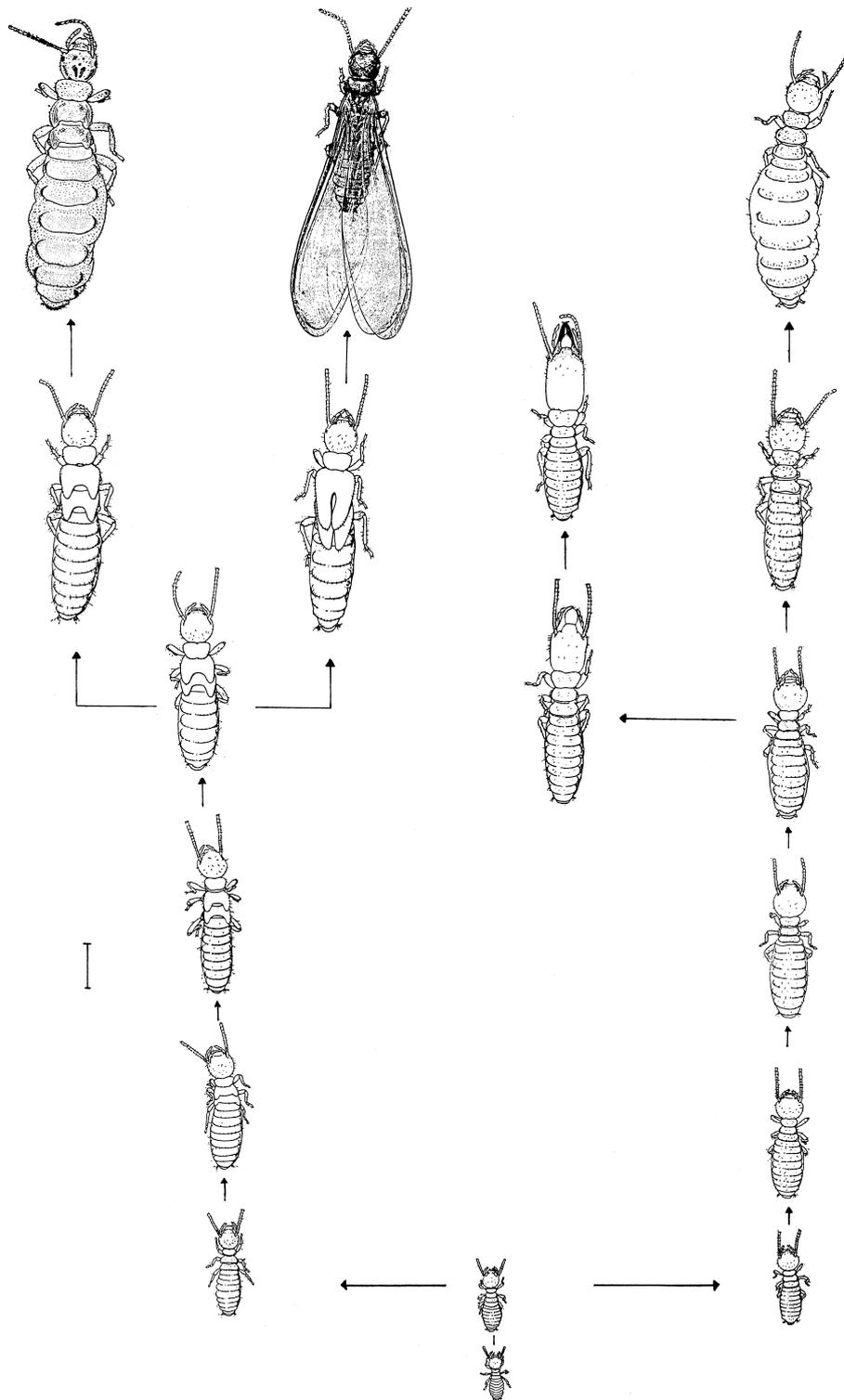
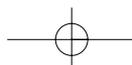
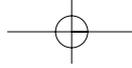


Fig. 1. Life cycle of *Reticulitermes* species according to F. Vieau (personal communication), amended from Buchli (1958) (L, larva; W, worker; N, nymph; LWBN, nymph with long wing buds; PBNEO, pre-brachypterous neotenic; BNEO, brachypterous neotenic).





in these studies was not stated and the number of eggs laid is dependent on colony size (see below). The eggs are often moved around and are continuously stacked and restacked. They are also polished and turned in the workers' mouthparts (Weesner, 1965). In young colonies, the eggs are initially attended by the reproductives and later by the workers (Grassé, 1949). Egg laying rates that have been quoted for *R. santonensis* include several thousand eggs per individual per year and 4.8 eggs per individual per hour (= 42,000 per year) (Grassé, 1949; Vieau, 1996), although the rate of egg laying is variable during the year. A period without egg laying occurs each year in termites from temperate regions (Grassé, 1949; Weesner, 1965; Nutting, 1969). The above rate of egg laying probably relates to mature colonies as *Reticulitermes* species have a very slow initial egg laying rate where young reproductives tend to lay five to six eggs in the first year and 25 to 30 eggs in the second (Feytaud, 1912; Snyder, 1926; Weesner, 1965). Thorne (1998) referred to various studies which showed that, in their first year, young *Reticulitermes* colonies reach no more than 30 individuals; Beard (1974) reported a figure of about 70 for colonies of *R. flavipes*.

There is considerable variation in the time required for egg development, varying from 15 to 55 days, at temperatures between 17 and 25°C (Grassi & Sandias, 1893; Feytaud, 1946; Buchli, 1950a; Weesner, 1956; Beard, 1974; Vieau, 1991). The period quoted by Buchli (1958) is 20–30 days at 25°C. Young termites emerge and pass through two larval stages or instars (Buchli, 1958; Thorne, 1996; Vieau, 1996). The first instar is approximately 1–2 mm long and can take between 7–17 days to develop; the second takes 10–18 days (Lespès, 1856; Weesner, 1956; Buchli, 1958; Vieau, 1991). First instar size is also said to vary depending on the environment (Buchli, 1950a). At the second moult, differentiation into the sexual and neutral lines occurs (Hare, 1934; Noirot, 1985; Noirot, 1990; Thorne, 1998). The worker line is thought to diverge irreversibly from the nymphal line, except for the ergatoids (see section on workers) (Thorne, 1998). The two lines can be differentiated at the third stage by the presence (in sexual) or absence (in worker) of wing pads (Feytaud, 1912). Some authors believe that caste determination (see below) occurs at the egg stage (Feytaud, 1912; Thompson, 1917; Snyder, 1925, 1926; Miller, 1969).

Workers

Workers are approximately 4–6 mm in length, wingless, have antennae with 14–17 segments, lack compound eyes, and have a pronotum that is trapezoidal in shape (Lespès, 1856; Feytaud, 1912; Snyder, 1926; Feytaud, 1946; Serment & Tourteaux, 1991; Vieau, 1991; Thorne, 1996). The definition of an isopteran worker according to Noirot & Pasteels (1987) is: '...morphologically specialised individuals whose development has diverged early and irreversibly from the imaginal line. Workers constitute a sterile, morphologically distinct, eusocial caste.' This definition proves difficult when it is considered that workers can become reproductives. A more appropriate term may be pseudo-worker. This would allow the differentiation between an individual that can develop into a soldier or an ergatoid.

Buchli (1958) (see fig. 6) observed nine worker instars, including the first two larval instars, after which the workers continued to moult but did not change in size (i.e. go through stationary moults). Harris & Sands (1965) and

Plateaux & Clément (1984) believed that there were a varying number of instars (five to seven from egg) in the Rhinotermitidae before the workers' heads become fully sclerotized. Juvenile cuticles are unsclerotized. These differences stem from the fact that the young worker instars are difficult to differentiate from the larvae (Grasse *et al.*, 1950). Termite workers are not necessarily in their final instar. They retain prothoracic glands and thus their capacity to moult into either a soldier or a supplementary reproductive with no wing buds (i.e. an ergatoid) (Noirot, 1985, 1988; Thorne, 1996). As mentioned above, this contradicts the earlier definition of a worker, which is supposed to diverge irreversibly from the sexual line. This is true if the sexual line is considered to be individuals with wing buds, but not so if they are considered to be individuals that are able to reproduce.

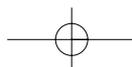
Workers start to feed during the third instar in a small colony and during the fourth instar in a large colony (Buchli, 1958). Workers can develop into soldiers from the fourth moult onwards (usually the sixth moult) and the seventh moult is the point at which development into ergatoids starts to occur (Buchli, 1951, 1958). Thompson (1917) was the first to suggest that ergatoids may be fertile workers. Ergatoids pass through two moults to develop from a worker and are approximately 7–9 mm in length (Noirot, 1990; Thorne, 1998). The differentiation of worker into an ergatoid can take 10 months, although it is thought to be faster in larger groups (Grassé *et al.*, 1950; Thorne *et al.*, 1999).

Workers are the most numerous caste and forage in order to feed the colony, as well as to tend the nursery and groom nestmates (Feytaud, 1911, 1912; Snyder, 1926; Noirot & Pasteels, 1987; Krishna, 1989; Vieau, 1996; Thorne, 1998). Their activity tends to increase in the early spring and decrease over the winter (Haverty *et al.*, 1999a). They also play a role in defending the colony and their aggressive behaviour has been well studied (Grassé, 1949; Buchli, 1961; Clément, 1978, 1986; Thorne & Haverty, 1991; Polizzi & Forschler, 1998; Haverty *et al.*, 1999b; Getty *et al.*, 2000). They have mouthparts that are adapted for chewing and possess flagellate protists in their hindgut that digest wood (Feytaud, 1946; Krishna, 1989). Workers are the first caste to develop when a new colony is founded by alates; their development takes about one year and they can live for several years. Buchli (1958) suggested that workers can live for 9–10 years in a natural situation, although little specific information is available on their longevity (Feytaud, 1912; Snyder, 1926; Nutting, 1969; Noirot, 1990).

Soldiers

Soldiers vary in length between and within species, for example, *R. flavipes* soldiers are 6–7 mm in length and *R. virginicus* (Banks) soldiers are 4.5–5 mm in length (Snyder, 1915; Buchli, 1958). Soldiers have a thorax and abdomen that resemble those of workers. They are blind and have biting mandibles for defence (Feytaud, 1912; Harris & Sands, 1965; Krishna, 1989; Serment & Tourteaux, 1991). Soldiers are thought to have a defence role, although in some cases they are rather passive and sometimes accompany workers on food scouting expeditions (Grassé, 1949; Thorne, 1998). They are completely dependent on the workers for food (Snyder, 1926; Harris & Sands, 1965).

Soldiers are present in higher proportions in young natural colonies. However, they are always outnumbered by



workers (Feytaud, 1920; Snyder, 1926; Feytaud, 1946). They usually make up 1–3% of a *Reticulitermes* species colony, although values of < 1% and 8–10% have also been reported (Hrdy, 1961; Haverty, 1977; Haverty & Howard, 1981; Grace, 1996; Forschler & Jenkins, 1999). Weesner (1956) stated that the number of soldiers present in a colony was influenced by environmental or genetic factors in the colony from which the initial reproductives originated. Noirot (1990) suggests that the proportion of soldiers present is dependent on the ecological niche that the termites occupy, with more soldiers being present in termite colonies that are more prone to predation. The formation of soldiers may also be artificially induced through the use of juvenile hormones and large numbers of soldiers are thought to be detrimental to the proper functioning of the colony (Hrdy & Kreck, 1972; Haverty & Howard, 1981).

There is no equivalent to the soldier caste in other social insects and it is the first to disappear when the colony is under threat (Feytaud, 1946; Noirot & Pasteels, 1988). *Reticulitermes* soldiers, as with all other castes, are comprised of both sexes and have rudimentary reproductive organs (Lespès, 1856; Feytaud, 1912; Grassé, 1949). Their lack of fertility may be due to the presence of prothoracic glands (Miller, 1969). As mentioned above, soldiers develop from workers and not from a special developmental line. This is true for all Heterotermitinae (Grassé *et al.*, 1950; Noirot, 1985; Vieau, 1996). Soldiers are formed in two stages from workers. After the first moult they form a white soldier (also called presoldier, callow soldier, pseudosoldier, soldier nymph or soldier larva), which is unpigmented and unsclerotized but with a soldier-like morphology. After the second moult a fully sclerotized soldier is formed, which does not moult again (Grassé, 1949; Harris & Sands, 1965; Weesner, 1965; Noirot, 1985; Noirot & Pasteels, 1987, 1988; Vieau, 1991; Thorne, 1996, 1998). Some authors believe that soldiers develop, via a pre-soldier stage, from the second instar larval stage (L2) to the fourth instar worker stage (W4) (Weesner, 1956; Plateaux & Clément, 1984). Noirot (1985) suggests that soldiers develop from any immature stage from the second stage onwards. Other authors suggest that soldiers develop from nymphs (Grassé, 1949; Buchli, 1958). The white soldier stage is reported to last 11–20 days (Weesner, 1965). This development is irreversible and, once the soldiers are formed, they are unable to regress to another caste (Thorne, 1996). There is little information available on their longevity (Noirot, 1990).

Nymphs

Nymphs are individuals with wing pads that develop into alates or secondary reproductives with wing pads (Harris & Sands, 1965). They have a similar role as the workers, and aid in the daily running of the colony (Noirot & Pasteels, 1987). Nymphs start forming 8 months after the nest has started (Grassé, 1949). Buchli (1958), however, stated that the nymphal line only developed in an *R. santonensis* colony when a minimum of 200 workers was present (i.e. after 18 months), and in an *R. lucifugus* colony when a minimum of 1000 workers was present (i.e. after four years). Weesner (1965) simply mentioned that a large colony is required for alate formation, and Grassé (1949) stated that nymphs formed when the alates were no longer present.

The number of antennal segments can be used to differentiate between instars. For example, nymphs (N6) have 17 antennal segments compared with 18 in secondary

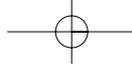
reproductives and alates (Feytaud, 1912; Buchli, 1958; Ionescu, 1959). It can be a problem using antennal segments to separate instars as they can often become damaged (Buchli, 1958).

The most recently postulated life cycle for *Reticulitermes* species has seven nymphal stages, including two larval stages that are common to both lines (Vieau, 1994a) (figs 1 and 7). After the first two larval stages (L1 & L2) the nymphs pass through four stages (N3 to N6) before either developing into nymphs with long wing buds (LWBN), which will develop into alates (primary reproductives), or nymphs with short wing buds that will moult into brachypterous neotenics (Vieau, 1994a). In *R. santonensis* N3 is distinguishable from other nymphal instars, whereas N4 to N6 cannot be separated (Vieau, 1999, 2001). In *R. lucifugus* the pre-neotenic brachypterous stage (PBNEO) is distinguishable earlier and is more easily separated from the other instars (Vieau, 1999, 2001). Noirot (1988) stated that the fourth instar nymphs were able to feed if they were not fed by workers but that this ability only lasted until the sixth instar. By contrast, Buchli (1958) thought that only the fifth and sixth instar nymphs were able to feed themselves. The amount of work carried out by a fourth instar nymph in a natural situation is negligible (Noirot & Pasteels, 1988).

The PBNEO stage was said by Buchli (1958) to be a stage seven nymph and the LWBN to be a stage eight nymph, which then becomes an alate. This idea, which was also supported by Noirot (1985), has been disputed by Vieau (1994a), who studied the evolution of the proportions of PBNEOs, LWBNs, BNEOs and alates in colonies, compared the individuals' histology and looked at levels of juvenile hormone and ecdysteroids. This led Vieau (1994a) to conclude that PBNEOs did not originate from the LWBNs but that both these stages originated from the stage six nymph (fig. 1). The apparent misinterpretation made by Buchli (1958) seems to be repeated by Thorne (1998), who implied that BNEOs are formed from pre-alate nymphs. Thus, it would suggest that the PBNEO develops into the LWBN. Grassé (1949) also caused confusion because he believed that there were three forms of neotenics, some with short wing buds, some with no wing buds and, finally, some with long wing buds. Vieau's (1994a) opinion is not a new one. It was first mentioned by Fritz Muller in 1887 (Pérez, 1895; Feytaud, 1912; Grassé, 1949) and repeated by Grassé (1949) who described two forms of N7 nymphs (his fourth instar), which were the same size but had wing buds of different lengths. Feytaud (1912) also believed this but stated the stage as being the fifth instar.

Neotenics

The most commonly found reproductive form in *Reticulitermes* species appears to be the neotenic (Feytaud, 1912, 1951; Bathellier, 1941; Vieau, 1991, 1993, 1994b, 1996, 2001; Thorne, 1998). Neotenics, supplementary or secondary reproductives that develop from nymphs or workers whose internal development is accelerated with only a few changes in external anatomy, are distinguished from nymphs and workers by their darker pigmentation, slight sclerotization, longer abdomen and the presence of eyes and ocelli (Weesner, 1965; Plateaux & Clément, 1984; Krishna, 1989; Serment & Tourteaux, 1991; Thorne, 1996, 1998). They show no wing development and retain many juvenile characteristics. Brachypterous neotenics in *R. lucifugus* are 12 mm in length (Thorne, 1998). There are conflicting views as to whether neotenics are able to feed themselves initially and



then lose this capacity, or whether they are never able to feed themselves (Snyder, 1925; Grassé & Chauvin, 1946). Certainly there seems to be a difference between *Reticulitermes* species, for example, *R. lucifugus* neotenics are able to feed themselves more readily than *R. santonensis* under laboratory conditions (L. Lainé, personal observation).

Secondary reproductives have been reported to be common in colonies of *R. santonensis* and *R. lucifugus* (Snyder, 1925; Feytaud, 1946; Vieau, 1991, 1994b), although Buchli (1958) was of the opinion that this caste only developed when there was a disturbance. Snyder (1926) believed that only secondary or primary reproductives were found in any given colony. Ergatoids seem to be rarely found in nature (Feytaud, 1946; Thorne, 1998). Brachypterous neotenics are not produced in the first few years following colony foundation (Weesner, 1965). The development of neotenics takes place from between 6 weeks to 4 months after a group of termites has separated from the main colony (Grassé, 1949; Thorne, 1998), though it is believed by some that in *Reticulitermes* species neotenics are formed in the presence of primary reproductives and several neotenics may be present in a single colony (Noirot, 1990; Serment & Tourteaux, 1991). Weesner (1956) did not believe that neotenics developed in the presence of primary reproductives. The process of forming new colonies by the formation of neotenics within a group of individuals that has been separated from the colony is commonly termed 'budding' (Pérez, 1907; Feytaud, 1946; Harris, 1958; Harris & Sands, 1965; Plateaux & Clément, 1984; Serment & Tourteaux, 1991). The extent to which budding occurs in nature is uncertain, although this is commonly observed in the field in France (Vieau, 1999). The first person to clearly explain the process of budding was Snyder (Snyder, 1912, 1920; Thorne, 1998; Thorne *et al.*, 1999). The groups of termites that bud off from a main colony and form a reproductive unit are termed 'satellite' colony units (Thorne *et al.*, 1999).

Egg laying starts approximately 4–8 weeks after the formation of neotenics has occurred (Feytaud, 1946). Female neotenics lay eggs at a lower rate than true queens. However, they are usually present in large numbers and therefore produce much larger communities, even though their egg-laying capacity is lower (Harris, 1958; Harris & Sands, 1965; Noirot, 1990; Thorne, 1996, 1998; Thorne *et al.*, 1999). Grassé (1949) thought this to be particularly true of the genus *Reticulitermes* where large numbers of neotenics are found. Conversely, Feytaud (1946), Pawson & Gold (1996) and Thompson (1917) reported that neotenics had a higher fecundity than primary queens, although Thompson (1917) went on to mention that this is only at the start of colony foundation and that the primary reproductives later overtake neotenics in terms of fecundity. The male to female sex ratio in *R. lucifugus* can vary from 1:1 to 1:15 (Feytaud, 1946).

Alates

Alates, the primary or first form reproductives (Thorne, 1996), develop approximately two years after colony foundation at set times during the year (Feytaud, 1920). There is usually only one batch formed per year, although there can be more in an urban environment due to more favourable environmental conditions, for example, higher temperatures resulting from central heating (Feytaud, 1912; Weesner, 1956; Krishna, 1989; Noirot, 1990). A period of warmth and increased humidity is reported to be required for alate development, however, not much information is

available with regard to alate dispersion or swarming (Pérez, 1907; Feytaud, 1912; Grassé, 1949; Weesner, 1956; Harris, 1958; Harris & Sands, 1965; Nutting, 1969). There is some disagreement with regard to when *R. santonensis* and *R. lucifugus* swarm, but in general this is between March and June (de Quatrefages, 1853; Lespès, 1856; Pérez, 1895; Feytaud, 1912, 1946; Buchli, 1956; Weesner, 1965; Vieau, 1994b). An increase in the proportion of alates compared with the proportion of neotenics is seen in *R. santonensis* as colony size increases (Vieau, 1994a). After swarming, the alates shed their wings along a suture, although this may occur without a flight, and then shortly afterwards pair and mate, each pair forming a new colony (Grassé, 1949; Krishna, 1989; Thorne, 1996). Swarming may or may not occur in *R. flavipes* colonies (Vieau, 1993; Thorne *et al.*, 1999).

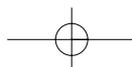
Nutting (1969) has reviewed flight and mating behaviour in great detail. The primary reproductives are initially able to feed. However, this ability is lost after the appearance of workers, who take over the duty of feeding the primary reproductives (Pérez, 1895; Krishna, 1989). Supplementary reproductives may be formed from alates that have had their wings removed and remain in the nest. In this case, the more correct term is an adultoid reproductive (Feytaud, 1912, 1946; Grassé, 1949; Harris & Sands, 1965; Thorne *et al.*, 1996).

Alates are imagoes that are fully sclerotized, dark brown to black in colour, winged, 8–10 mm in length (including wings) with compound eyes (Feytaud, 1912; Banks & Snyder, 1920; Krishna, 1989; Thorne, 1996, 1998). Males and females can be identified using the following characteristics (Lespès, 1856; Feytaud, 1912, 1946; Grassé, 1949; Weesner, 1956, 1965; Hickin, 1969).

1. The female has an enlarged seventh sternite covering the eighth and ninth sternites.
2. The male has a seventh sternite that is similar to the previous sternites and a pair of styli on the ninth sternite.

The de-alated female primary reproductive can become physogastric (i.e. develop a distended abdomen), but these are rare and do not reach the proportions found in the Termitidae (Grassé, 1949; Thorne, 1996). Physogastric females (queens) stay relatively mobile (Lespès, 1856; Feytaud, 1912; Snyder, 1926; Feytaud, 1946). Primary reproductives normally live for 7–10 years (Thorne *et al.*, 1999) and up to 18 years in a natural environment (Feytaud, 1946), and have been observed to survive for 25 years in artificial colonies (Snyder, 1926).

Physogastric queens have not been reported in *R. santonensis*. In the urban habitat, where this species is mainly found, colonization tends to occur via budding. Vieau (1996) considered that though swarming occurs in *R. santonensis*, colony establishment by alates is never successful. This has been suggested to be an indication that this species is in the process of establishing itself and is therefore an introduced species (Vieau, 1993, 1999). It is also possible the swarms are successful, but that the physogastric queens are rarely found due to their cryptic habit. This apparent lack of swarming may be comparable to that seen in tramp species of ants where the ability for nuptial flights has been lost (Passera, 1994). Weesner (1965) mentioned having witnessed all three forms of reproductive types of *R. flavipes* in the USA. However, relatively few observations are available on the behaviour of reproductives present in the wild (Vieau, 1999, 2000), although swarming of *R. hageni* (Banks) and *R. virginicus* in the USA has been well documented (Weesner,



1970). Buchli (1958) concluded that swarming was unlikely to be successful in *R. lucifugus*, although this is probably because he confused *R. lucifugus* with *R. santonensis* (Vieau, 1999). *Reticulitermes lucifugus* in Italy, where *R. santonensis* does not occur, has been reported to swarm successfully (Grassi & Sandias, 1893; Feytaud, 1912; Snyder, 1926).

Pseudergates

Reticulitermes species occupy an intermediate stage in the evolution of life cycles in termites (Noirot & Pasteels, 1988). Workers separate from the sexual line at the third instar, however, nymphs in the sexual line can also develop into pseudergates (Harris & Sands, 1965; Noirot & Pasteels, 1988). Pseudergates are defined as individuals that have diverged from the sexual line at a late instar by undergoing a regressive moult (where some nymphal characteristics are lost) or a stationary moult (where growth occurs without changes in morphology) and have stabilized to a state where they function as workers (Grassé *et al.*, 1950; Noirot, 1985; Noirot & Pasteels, 1987, 1988; Vieau, 1991; Thorne, 1998). Pseudergates have greatly reduced or no wing buds (Noirot, 1985; Noirot & Pasteels, 1987; Krishna, 1989) but never regress to true worker morphology (Noirot, 1985). They conserve the ability to develop into neotenics, alates or soldiers and are usually present in conjunction with workers (Grassé *et al.*, 1950; Buchli, 1958; Thorne, 1998). Pseudergates are present in very low numbers in *R. lucifugus* colonies (4–5%) and have not been found in *R. santonensis* colonies (F. Vieau, personal communication).

Some reviewers have used the term 'pseudergates' for 'worker' (Weesner, 1956; Grace, 1996; Pawson & Gold, 1996). This may be due to the difficulty of differentiating between workers and pseudergates. The identification of workers cannot, therefore be limited to the absence of wings buds and the presence of a pigmented gut (Noirot & Pasteels, 1987). Pseudergates can be distinguished from workers morphologically by the fact that their pronotum is narrower than their mesonotum (Buchli, 1958).

Caste determination

Caste differentiation in termites is thought to occur mainly during post-embryonic development. Various authors have suggested that the developmental pathway taken by termites depends on dietary or environmental factors (Grassi & Sandias, 1893; Pérez, 1907; Thompson, 1917; Hare, 1934; Grassé, 1949; Buchli, 1956; Luscher, 1960; Weesner, 1965; Esenther, 1969; Noirot, 1990), whereas Snyder (1925) and Thompson (1917) suggested that caste development was determined within the embryo. Grassé (1949) proposed that there were two mechanisms involved in caste differentiation: (i) sociohormones whose formation inhibited the presence of certain castes; and (ii) sensoral stimuli that have been seen to have an effect on ovarian activity in worker *Polistes* (Hymenoptera: Vespidae). However, the exact mechanisms involved in caste development are still unknown (Noirot, 1990) and research in this area is clearly required.

Comparisons of life cycle pathways

A variety of possible life cycles (figs 1–8) have been proposed for *Reticulitermes* species (Grassi & Sandias, 1893;

Snyder, 1915; Hare, 1934; Feytaud, 1946; Grassé, 1949; Buchli, 1958; Noirot, 1985; Vieau, 1991, 1994a). However, in most cases, the literature does not provide detailed drawings or descriptions of the various stages and the most widely accepted study on the life cycle remains that of Buchli (1958). It is important to consider the difficulties involved in studying termite life cycles. Marking termites, by using paints or through consumption of dyes, may influence termite behaviour and survivorship. Yet without using some form of marking it is impossible to follow individuals through their developmental stages as, at least in the early stages, termites need to be fed by older individuals. In the later stages of development it is possible to study groups of individuals at the same stage, however, these soon start to differentiate.

The first diagram depicting the life cycle of a *Reticulitermes* species is that of Snyder (1915) (fig. 2). The same ideas were presented by Feytaud (1946). Both were based on the work of Grassi & Sandias (1893). The inclusion of 'large-headed' larvae is common to these studies.

The life cycle diagram shown in fig. 2 differs markedly from the simplified life cycle diagram of Hare (1934) (fig. 3). Hare suggested that there were three or four worker instars before differentiation into the 'adult worker' and the pre-soldier. The adult reproductive was said to pass through five nymphal instars prior to development into an alate. There were two larval instars before the split into the two lines, as in *Coptotermes* species (Roisin & Lenz, 1999). Hare (1934) does not mention the presence of neotenics.

In contrast, Grassi & Sandias (1893), Snyder (1915) (fig. 2) and Feytaud (1946) (fig. 4) considered that there was only one undifferentiated larval instar and that the second larval instar could be differentiated by the size of the head into individuals in the 'neutral' or sexual line. This idea was supported by Grassé (1949) in his model pathway (fig. 5). Larvae with small heads were assumed to develop along the sexual line and those with large heads along the 'neutral' line. In this pathway the split into the neotenic and the imagal lines occurred at the second moult, with two types of neotenics probably formed from workers and nymphs with short wing buds. Alates were said to develop from nymphs with long wing buds. The major difference from the most

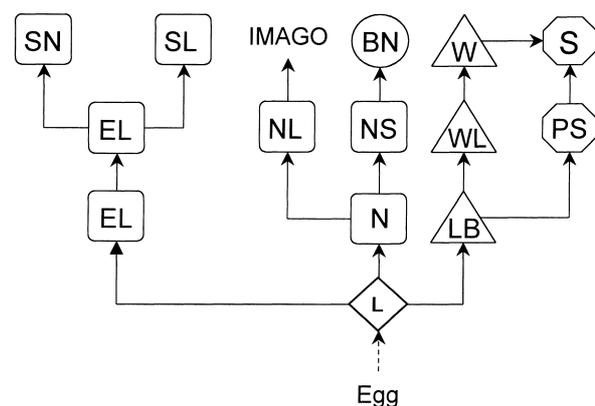


Fig. 2. Life cycle of *Reticulitermes* species based on Snyder (1915) (LB, larva with large head; EL, emergency reserve reproductive; WL, worker larva; NL, nymph with long wing buds; NS, nymph with short wing buds; SL, emergency larval substitute; SN, emergency nymphal substitute; BN, brachyperous neotenic; PS, pre-soldier; S, soldier).

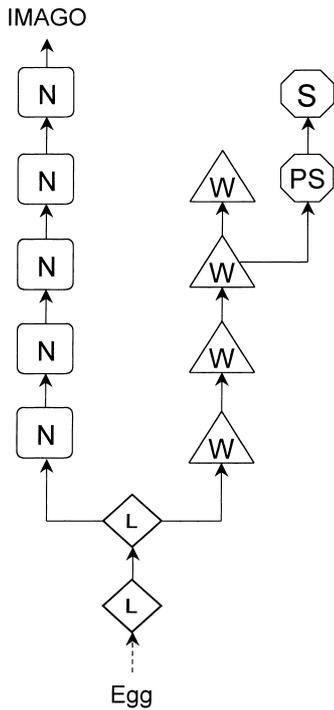
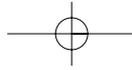


Fig. 3. Life cycle of *Reticulitermes* species based on Hare (1934) (for nomenclature see figs 1 and 2).

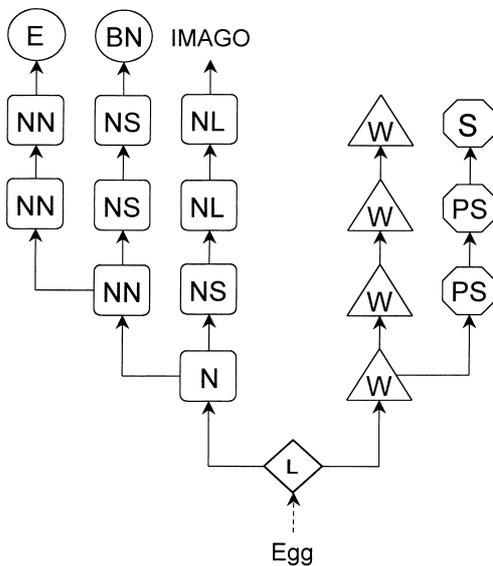


Fig. 4. Life cycle of *Reticulitermes* species based on the description by Feytaud (1946), taken from Grassi & Sandias (1893) (NN, nymph with no wing buds) (see figs 1 and 2 for nomenclature).

recent theory on the post-embryonic development of *Reticulitermes* species (Vieau, 1991, 1994a) (figs 1 and 7) is that the ergatoid develops from the nymphal line in Feytaud's (1946) pathway (fig. 4), whereas Vieau believes it develops from workers. There is also some disagreement over the number of moults that occur for development into

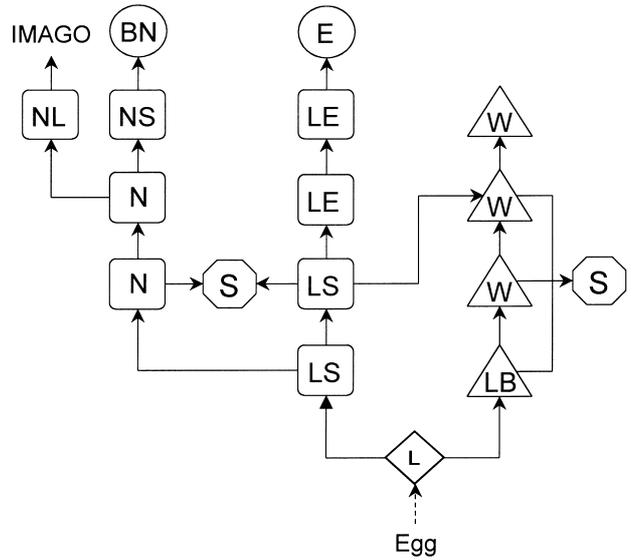


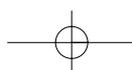
Fig. 5. Life cycle of *Reticulitermes* species based on the description by Grassi & Sandias (1893) and later by Grassé (1949) (LS, larva with small head; NE, neotenic larva) (see figs 1 and 2 for nomenclature).

the different stages, almost certainly due to the difficulty in identifying individuals of the different stages.

Feytaud (1946) and Grassé (1949) (figs 4 and 5) confused the sexual and neutral lines. They showed a cross-over from what they considered to be the sexual line (individuals developing from small-headed larvae) and the worker line (individuals developing from large-headed larvae). Although these two developmental pathways are considered incorrect today, they cannot simply be disregarded as they still may play a role in improving our knowledge of the life cycle. The most recent theory (figs 1 and 7) shows the ergatoids or third form reproductives developing from the worker line, whereas in fig. 5 all three types of reproductive originate from a nymph or small-headed larva. Grassé (1949) (fig. 5) also assumed that soldiers came from the sexual line, while Buchli (1958) (fig. 6) suggested soldiers could develop from both the sexual line and the worker line. In the most recent theories soldiers originate from the worker line (Noirot, 1985; Vieau, 1991).

Buchli's 1958 interpretation of the *Reticulitermes* life cycle (fig. 6) is somewhat complex. His work describes the ontogenetic 'potential' of *R. santonensis* and *R. lucifugus* and included various developmental pathways which are not now thought to occur in nature (Noirot, 1985; Noirot & Pasteels, 1987; Vieau, 1994b). His was the first life cycle diagram where the presence of pseudergates was shown. Brachypterous neotenic were shown to develop from either pseudergates or from later nymphal instars. Noirot (1985) (fig. 8) later simplified Buchli's life cycle excluding the pseudergates and neotenic, which are the least understood castes in terms of their development. The life cycle (fig. 8) is virtually identical to that of *Reticulitermes speratus* (Kolbe) developed by Takematsu (1992), however, in the latter, the pre-soldiers develop from one stage later (i.e. W4 and W5 instead of W3 and W4).

The most recent theory (figs 1 and 7) supports a division at the sixth instar of the sexual line into either alates or



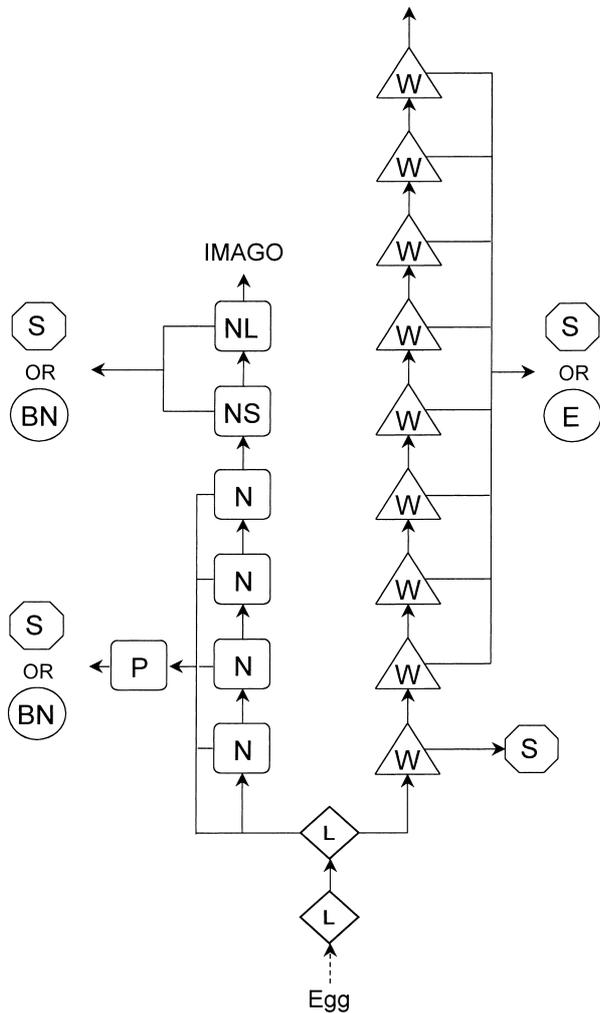


Fig. 6. Ontogenic potential of *Reticulitermes* species based on the description by Buchli (1958) (P, pseudergate) (see figs 1 and 2 for nomenclature).

BNEOs. The nymphs with long wing buds (LWBN) develop into alates and the PBNEOs develop into BNEOs. The ergatoids develop from the sixth or seventh instar of the worker line and the soldiers develop from the sixth instar in the worker line. Development of pseudergates is assumed to follow the pathway described by Buchli (1958) (fig. 6).

Conclusions

There have been many changes with regard to the interpretation of the life cycle of *Reticulitermes* species (figs 2–8). The life cycle that is most frequently referred to remains that of Buchli (1958) although this has some methodological flaws. The most recent update to the life cycle, by Vieau (1994a) (figs 1 and 7), is presently the most accepted life cycle for *R. lucifugus* and *R. santonensis* in the French scientific community. However, it is likely that the development of any single individual may be more complex than the linear development presented in these figures. Individuals, for example, can regress from the sexual line to become pseudergates.

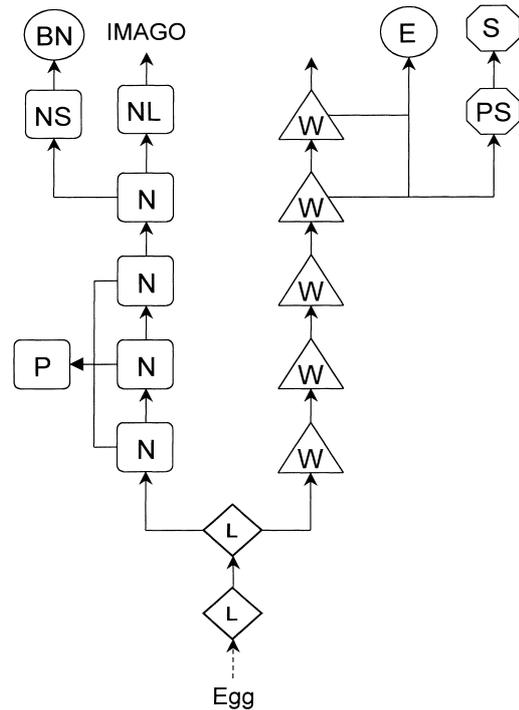


Fig. 7. Life cycle of *Reticulitermes* species based on the description by Vieau (1991, 1994a, personal communication) (see figs 1 and 2 for nomenclature).

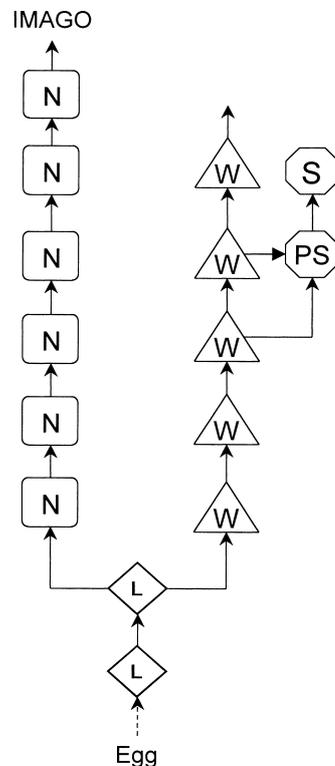
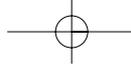


Fig. 8. Life cycle of *Reticulitermes* species based on the description by Noirot (1985) (see figs 1 and 2 for nomenclature).



Some investigators have concentrated on details of the life cycle but failed to establish the number of stages involved (Lespès, 1856; Noirot, 1985; Serment & Tourteau, 1991; Thorne *et al.*, 1999). This causes difficulty when comparing different models, as there is considerable inconsistency, particularly concerning the number of moults required for development into workers and soldiers. Development to what may be considered the 'final' stages could require many more moults than those shown in any of the life cycle pathways. There is also a need for researchers to agree on a standard terminology.

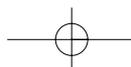
There is clearly much that remains to be investigated in the area of *Reticulitermes* life cycle biology. Biochemical and molecular genetic approaches may be particularly useful. One area that requires clarification is the development of sexual reproductives from a supposedly 'neutral' worker line. It is suggested here that the term 'neutral' line is no longer valid and that the term pseudo-worker line should be used instead. There are also known differences between *Reticulitermes* species, yet they are still assumed to have the same life cycle. The literature is made even more difficult to interpret as statements are often made about the genus rather than specifying individual species. Many of the discrepancies observed in the literature are probably due to the marked inter- and intraspecific plasticity of *Reticulitermes*.

Acknowledgements

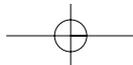
The authors thank the Forestry Commission (UK) for financial support and Hugh Evans and Robert Verkerk for their support and advice. The comments of Florent Vieau, Brian Forschler and Robert Butcher was also much appreciated.

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Appendix 1

Glossary

Term	Synonym	Definition
Larva	White immature	First two stages after hatching.
Worker	–	Individual with no wing buds, in the neutral line whose main role it is to feed the colony. Also has role in defence.
Pseudergate	–	Individual that has regressed from the sexual line and performs similar functions to the worker.
White soldier	Pre-soldier, callow soldier, soldier larva, pseudosoldier, soldier nymph	Stage between a worker and a soldier.
Soldier	–	Individual that develops from the neutral line that defends the colony.
Nymph	–	Instars with wing buds, in sexual line which will eventually develop either into a brachypterous neotenic or an alate.
Ergatoid	Apterous neotenic, third form reproductive	Reproductive with no wing buds that develops from the neutral line.
Brachypterous neotenic	Second form reproductive	Reproductive with small wing buds that develops from the sexual line via a seventh instar pre-brachypterous neotenic nymph.
Alate	Imago	Reproductive with wings that develops from the sexual line via a seventh instar long wing bud nymph.
Primary reproductive	First form reproductive	Alate which has formed a new colony after having lost its wings.
Secondary reproductive	–	Reproductive other than a primary reproductive.
Supplementary reproductive	–	Brachypterous neotenic or ergatoid formed in the presence of a primary reproductive.



Erratum

REVIEW ARTICLE

The life cycle of *Reticulitermes* spp. (Isoptera: Rhinotermitidae): what do we know?

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Bulletin of Entomological Research, Vol. 93(4), pp. 267–378

Following an error in the production process of the above paper, Figure 1 was printed without its annotations. Please replace with the correct version opposite.

Reticulitermes life cycle

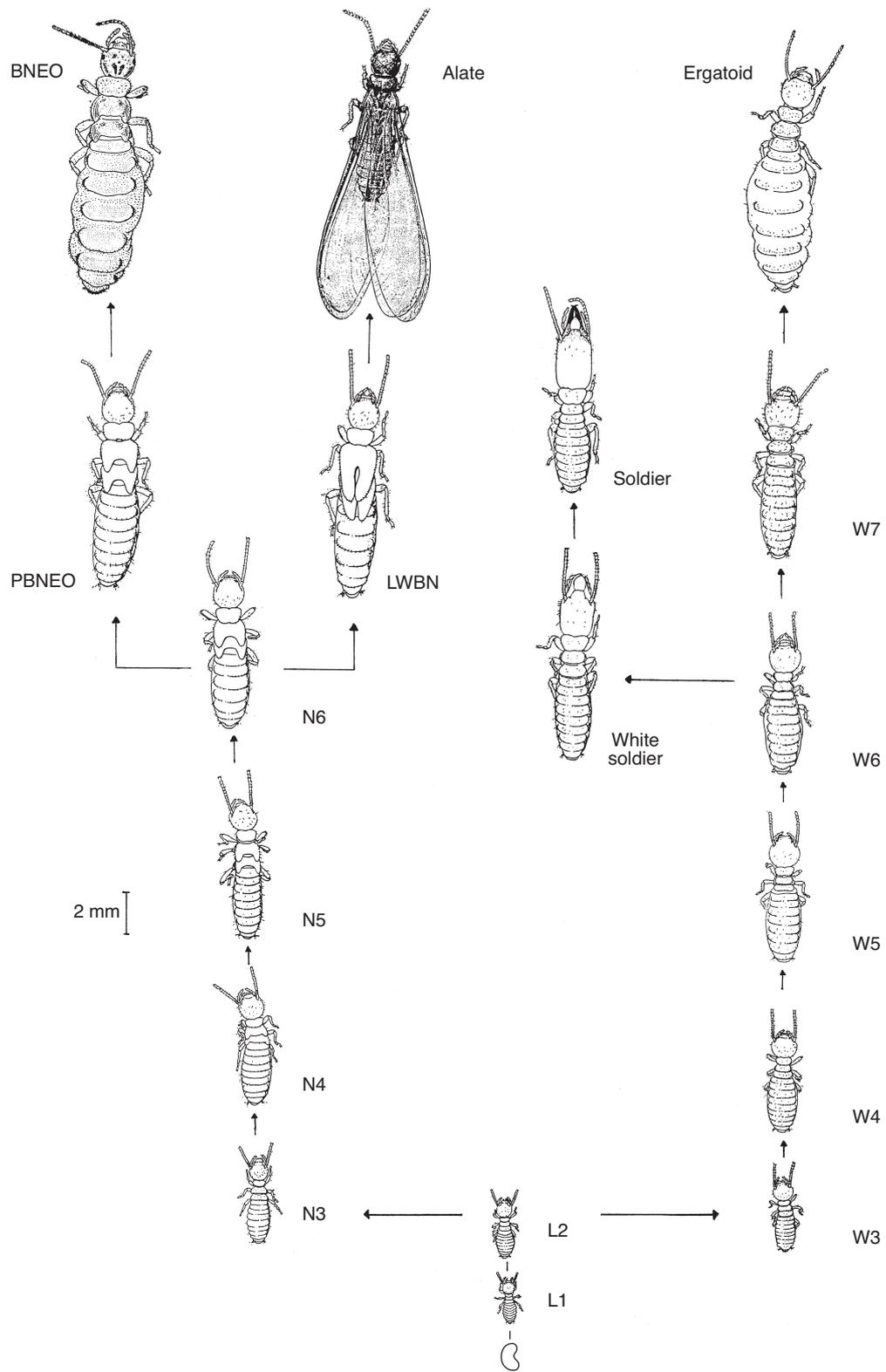


Fig. 1. Life cycle of *Reticulitermes* species according to F. Vieau (personal communication), amended from Buchli (1958) (L, larva; W, worker; N, nymph; LWBN, nymph with long wing buds; PBNEO, pre-brachypterous neotenic; BNEO, brachypterous neotenic).