



The evolution of eusociality in termites

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This talk

- Introduction to termites
- Eusociality requirements
- The phylogenetic evidence
- The evolution of castes

Termites

- Eusocial Dictyoptera
- Complex social structures (workers, soldiers, alates)
- Feed on dead plant material (wood, litter, humus, soil) or, less commonly, living plant material (grass, micro-epiphytes, roots etc.)
- Complex mutualisms within gut (all termites) or outside (fungus-growing termites) with
- Highest diversity in tropical rain forests
- Major players in decomposition, soil structure, and energy flow

Termites

- All fully eusocial (but see later...)
- All have alates, most have soldiers, a majority have workers
- Almost all feed on dead plant material, at various stages of decay
- Diplo-diploid genetic system
- As importantly, they're not *ants*!



Traditional termite Classification

- Traditionally an Order (Isoptera)
- split into 7 families:
 - Mastotermitidae (N Australia, detritus)
 - Hodotermitidae (Old World deserts, grass)
 - Termopsidae (temperate rain forests, wood)
 - Kalotermitidae (rainforest canopy, wood)
 - Serritermitidae (S S America, ?cleptoparasite)
 - Rhinotermitidae (Cosmopolitan, wood)
 - Termitidae (Pantropical, varied, 60% of spp, subfamily classification)

Alates

- Winged, male and female reproductives
- Produced in large numbers, usually at beginning of rainy season
- Pair up on ground and form new colony in soil or in dead wood
- Pair for life and mate throughout lifetime

Soldiers

- Have one function – defending the colony
- Very wide range of head morphology

Workers

- Do most of the rest of the work of the colony
- Feeding, building, tending

An anomaly

- Hamilton proposed:
 - Eusociality may evolve if $br_s > r_0c$
- This gives Hymenoptera an apparent head start as $r_s = 0.75$, for sister workers
- But in termites $r_s = 0.5$ for both brother and sister workers
- So, an apparent problem, as termites are ALL eusocial
- This has lead to many ingenious attempts to make termites 'haplo-diploid' (ring chromosomes, inbreeding)

Necessary conditions for eusociality

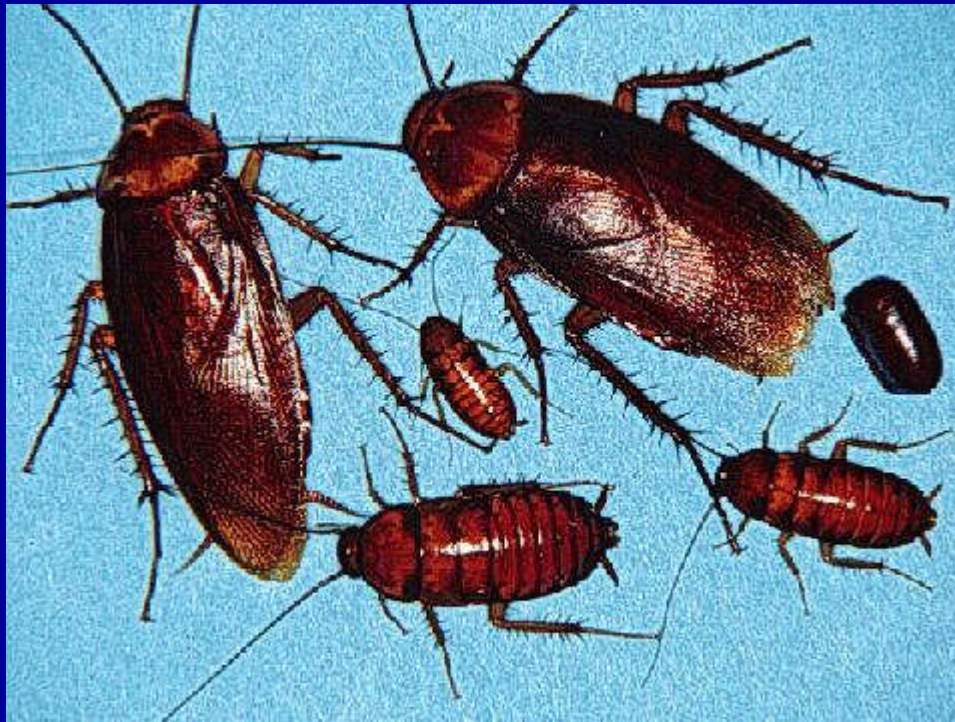
- Lifetime monogamy
- Overlapping generations
- Some basis for $b > c$

- Phylogenetic evidence for this?

Phylogenetic background

- Well established that termites, mantids and cockroaches form a monophyletic group: the Dictyoptera.
- Three competing hypothesis within Dictyoptera
 - termites, (mantids, cockroaches)
 - mantids, (termites, cockroaches)
 - mantids, (cockroaches including termites)

Dictyoptera



Biological background

- Termites are diploid, xylophagous, hemimetabolous insects
- All extant species are eusocial:
 - overlapping generations
 - sterile ‘functional’ caste (soldiers and/or workers)
 - (however, not all have soldiers, some may not have helper ‘workers’, Korb)

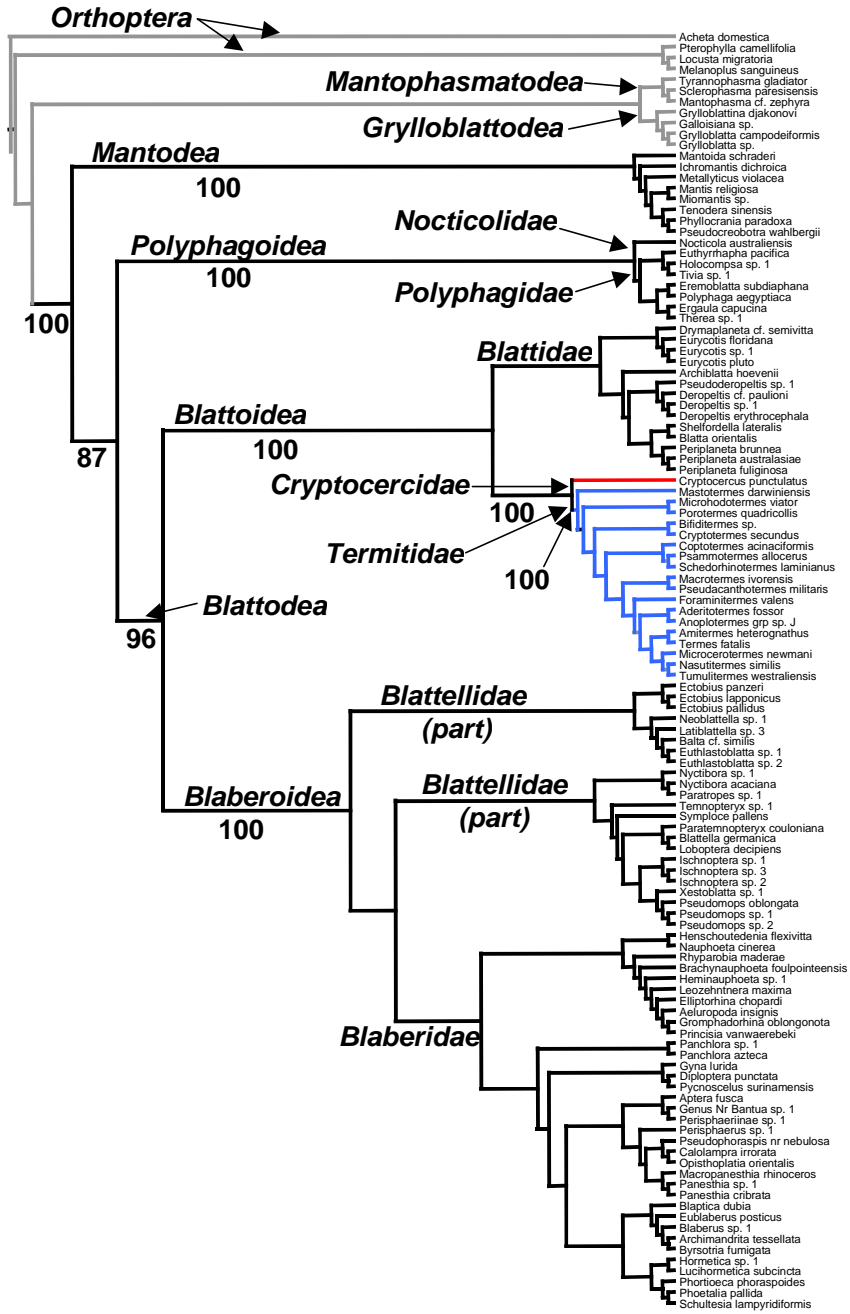
Key controversy in understanding early social evolution of termites

- Cleveland (1930s) showed that social wood-roach *Cryptocercus* had the same specialised gut flagellates as termites.
- Strong candidate, therefore, to be sister group of the termites.
- Arguments have since then focused on:
 - position of *Cryptocercus* within cockroaches
 - relationship between *Cryptocercus* and termites
- ARE TERMITES COCKROACHES?
- If so – this changes ideas a lot...



Molecular evidence

- Lo, Legendre, Klass, Inward (most comprehensive) all agree key points
- >100 Dictyoptera: all subfamilies of termites and cockroaches, representative mantids, outgroups
- Five genes: two nuclear (28S and histone 3), three mitochondrial (12S, 18S and COII)
- Phylogenetic trees



Summary

- Termites are sister to *Cryptocercus*
- This clade is within the Blattoidea
- Blattoidea is within the Blattodea (cockroaches)
- All of these relationships are very strongly supported

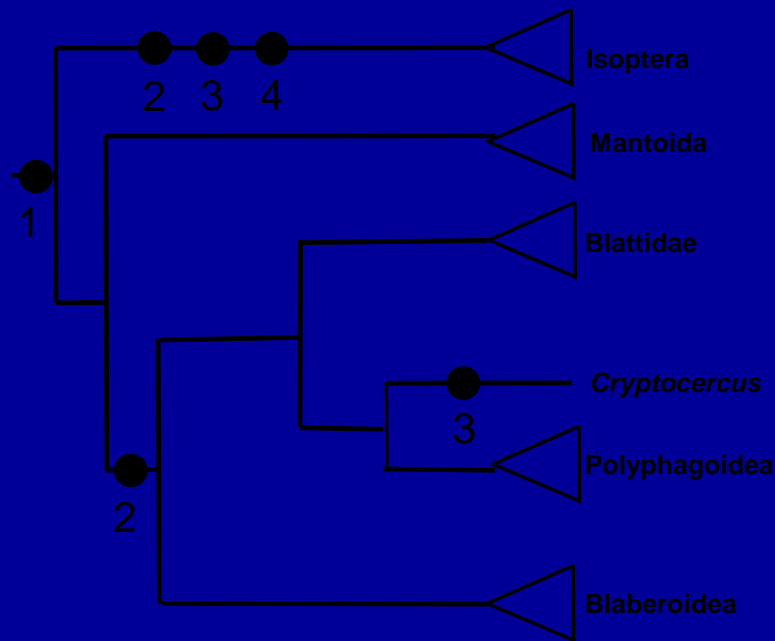
How this changes views about social evolution of termites

- All extant termites are eusocial, in the sense of having pre-imaginally determined sterile castes
- Earlier phylogenetic hypotheses left termites on a limb: eusociality emerged fully-formed from nowhere
- Great advantage of the ‘termites-as-cockroaches’ hypothesis is that we have a phylogenetically well-supported hypothesis of transformation (Nalepa and Bignell)

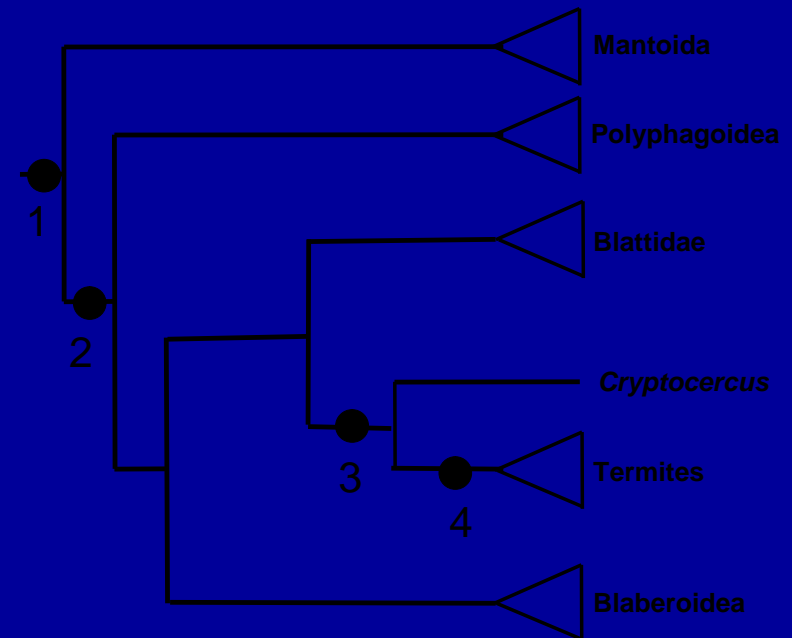
Proposed steps (Nalepa / Bignell)

- 1: ootheca formed from secretions of the asymmetrical accessory glands
- 2: ootheca formed internally in vestibulum, keel pointing upwards until deposited
- 3: wood-feeding, unique hypermastigid and oxymonad gut flagellate assemblages, biparental care, proctodeal trophallaxis, monogamy
- 4: male genitalia bilaterally symmetrical and much reduced, sperm immotile or weakly motile, true soldier caste, overlapping generations with reproductive division of labour ('eusociality').

Old hypothesis



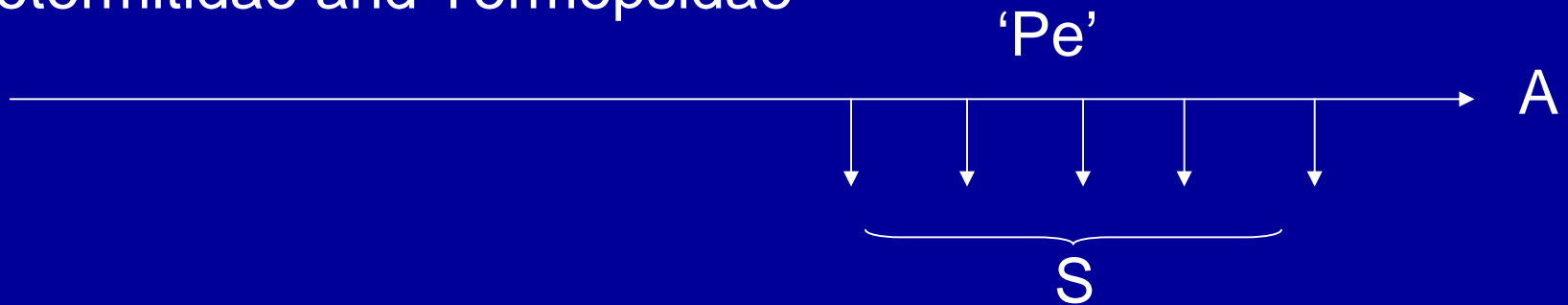
New hypothesis



- 1: ootheca formed from secretions of the asymmetrical accessory glands
- 2: ootheca formed internally in vestibulum, keel pointing upwards until deposited
- 3: wood-nesting, unique hypermastigid and oxymonad gut flagellate assemblages, biparental care, proctodeal trophallaxis
- 4: male genitalia bilaterally symmetrical and much reduced, sperm immotile or weakly motile, true soldier caste, overlapping generations with reproductive division of labour.

Caste determination

Kalotermitidae and Termopsidae



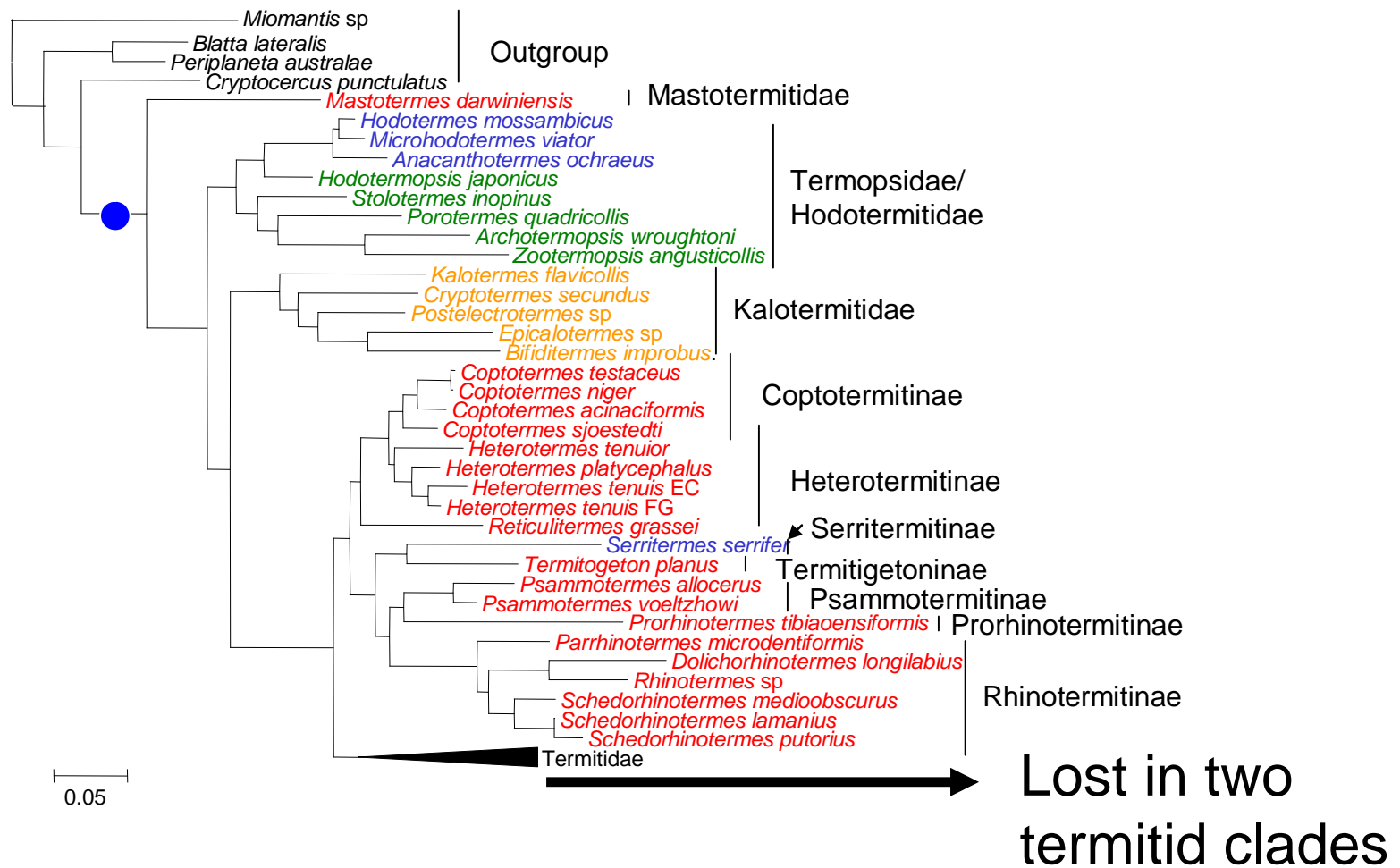
~ all other families



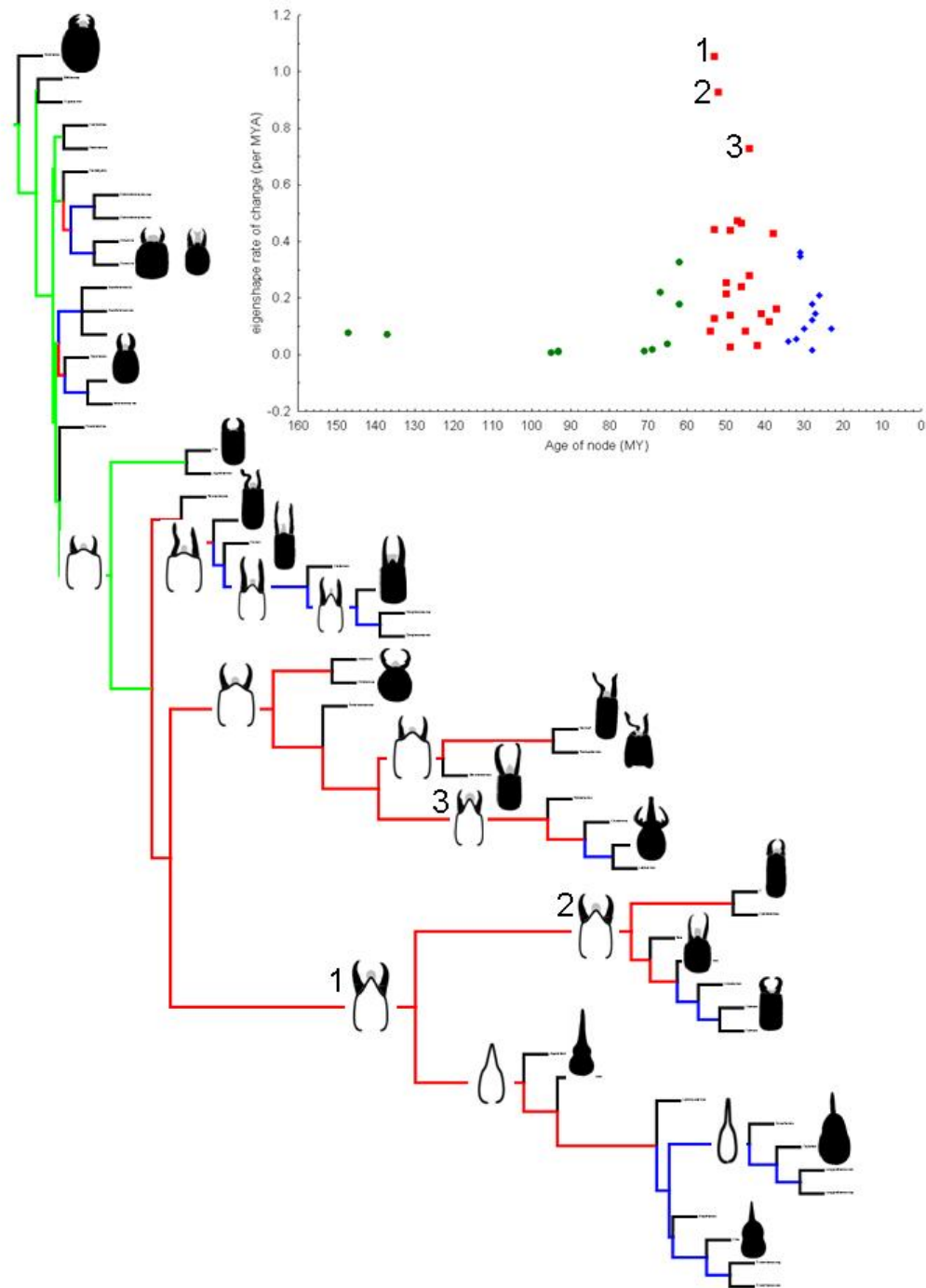
Origins and stability of castes: soldiers

- Soldiers are monophyletic, all sterile
- Soldiers have been lost twice: but only in the Termitidae (very recent groups)
- Soldiers evolved for defence against conspecific colonies? Now used extensively for defence against ants
- Soldier diversification almost entirely in one clade – the Termitidae

Soldiers



- Soldiers evolved



Soldier diversification

Possibly in response to diversification of ants in early tropical rain forests

Loss of soldiers

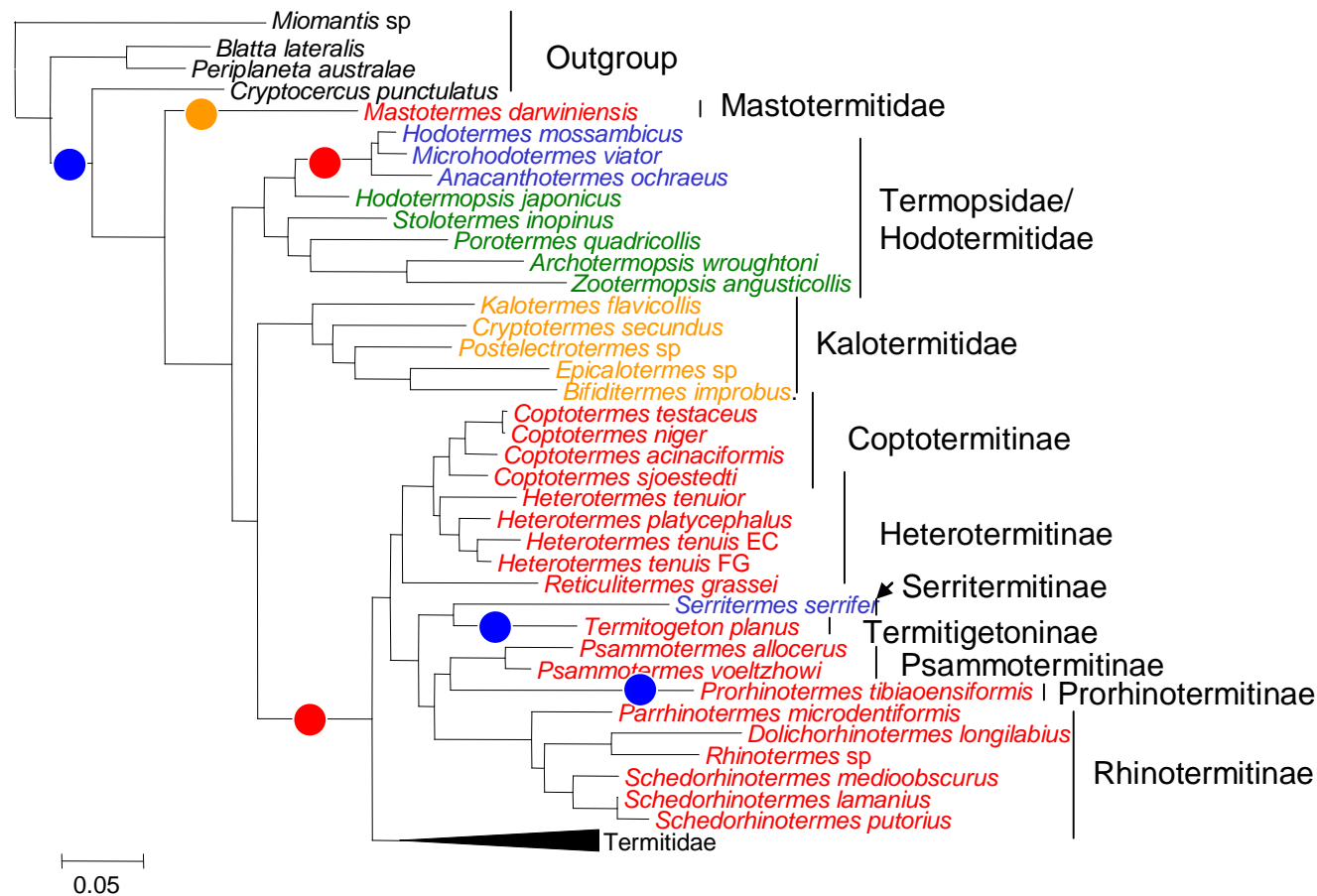
- Correlated with a reduction in colony size?
- Coincides with evolution of suicidal ('autothysic') workers
- Converge on hymenopteran workers



Origins and stability of castes: workers

- True workers (normally no potential to develop into adults) have probably evolved three times in different 'flavours'
- have potentially been lost once or twice
- Helpers don't always help

Workers



- true workers- simple developmental pathway, helpers
- No true workers - don't help (much)?
- true workers- definite helpers: EUSOCIAL

Summary (workers)

Clade	True workers	Central nest
Mastotermitidae	'Yes'	Yes
Termopsidae	No	No
Hodotermitidae	Yes	Yes
<i>Termitogeton</i>	No	No
<i>Prorhinotermes</i>	No	No
Other Rhinotermitidae	Yes	Yes
Termitidae	Yes	Yes

Complete correlation

Are all termites eusocial?

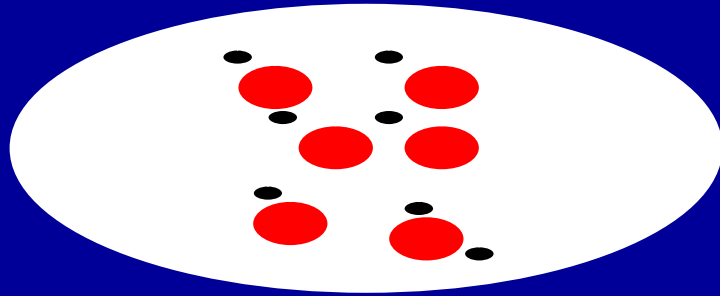
- Depends – there are no species which have neither *workers* nor *soldiers*.
- Present model suggests that termite soldiers evolved first to defend colonies against other termites
- Workers evolved (convergently) only after central nesting evolved

Explanations?

- Soldier evolution linked to colony defence
- True worker evolution linked to foraging from a central nest

Synthesis

- Complex, but can, perhaps, be linked to
 1. Shifts to and from wood nesting to central nesting
 2. Intra-colony defences
 3. Chances of colony fusion

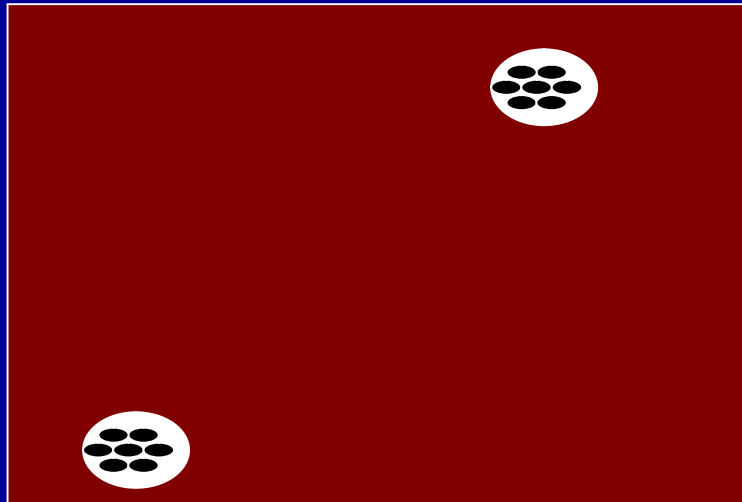


Blattidae

Detritus: ubiquitous, low value, dangerous

Semi-social, groups, with coprophagy, generally $b < c$, as can disperse to find other equivalent resources

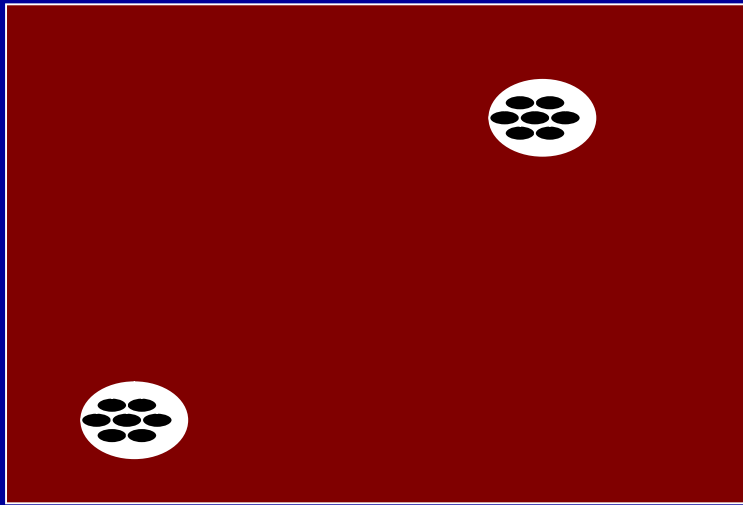
Unique flagellates
Wood feeding



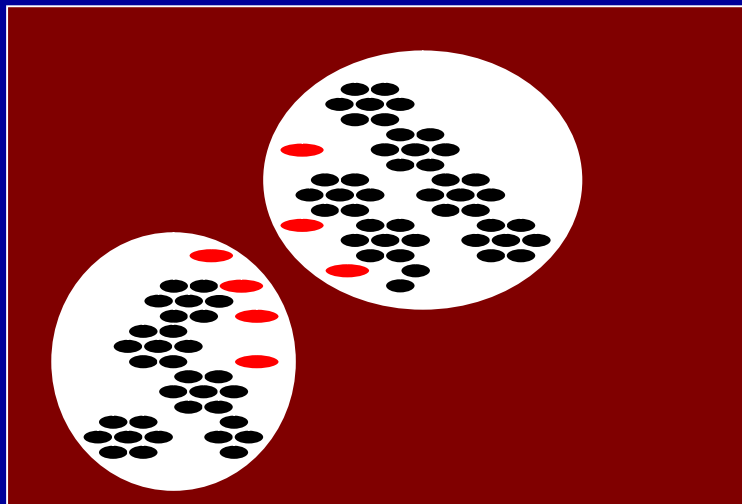
Dead wood: patchy, concentrated, safe

Small family groups with offspring tied to parents by (a) need to pick up flagellates in final moult, (b) cost of leaving high value resource. But offspring DO eventually disperse.

Cryptocercus



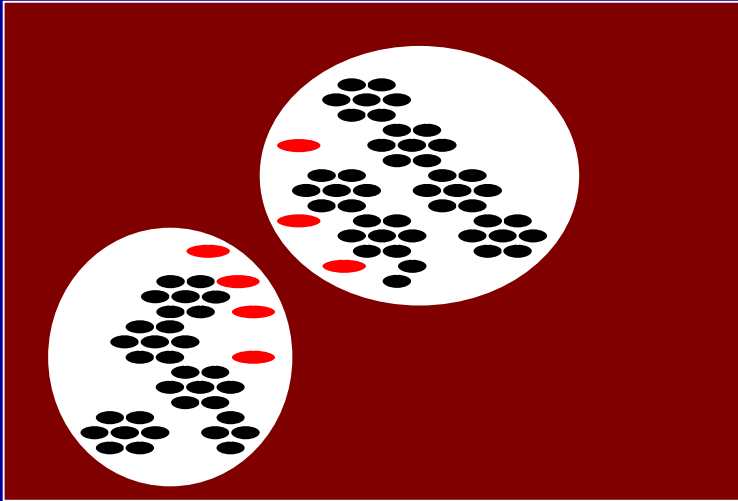
Increasing digestive efficiency
Colony expansion



Soldier evolve to protect colony.
First true sterile adult caste,
 $b \gg c$, as can never inherit or
leave.

Totipotent immatures can decide
to stay or leave based on b and
 c .

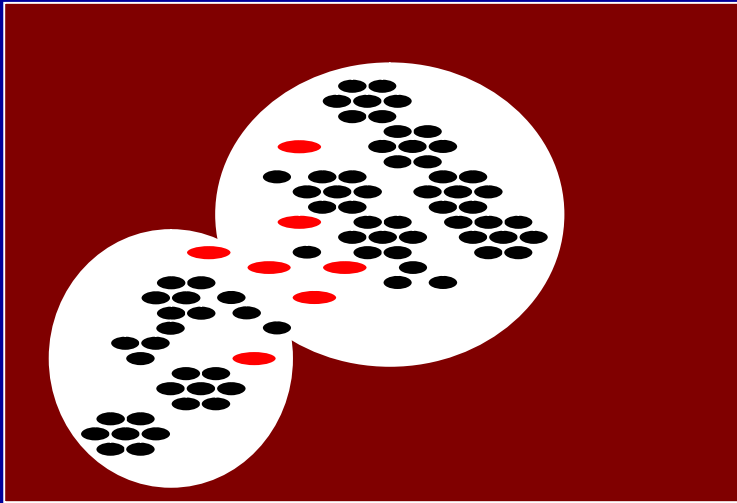
Termopsidae and Kalotermitidae classic form



Soldiers: only inclusive fitness benefits

Workers: three fitness opportunities

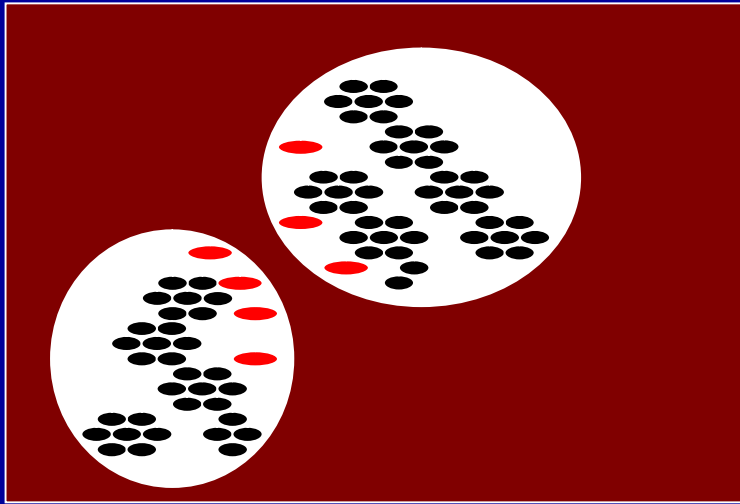
1. Inclusive fitness, as soldiers, don't mature, help
 2. Stay and hope to inherit (incl. 'accelerated inheritance')
 3. Mature, disperse
- (In studied systems, 2, seems to predominate, as immatures don't help much)



Colony fusion prevents Full worker eusociality?

When colonies fuse:

1. Primary reproductives are often killed
2. Immatures stay, and some develop into reproductives that may take over the colony ('accelerated inheritance')
3. Very few disperse
4. However, Korb's work suggests that many stay whatever happens, but the number that stay is correlated with relatedness with controlling reproductives (inclusive fitness)

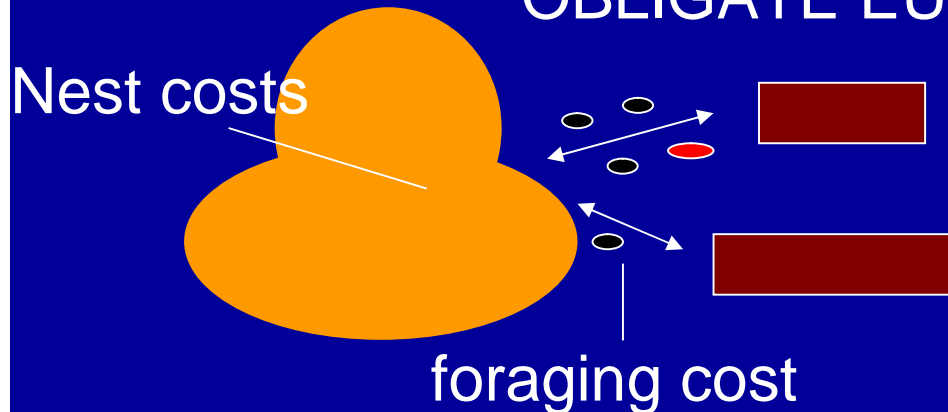


Problem with single wood piece is competition.
Obviously with other termites but also, more importantly perhaps, with fungi.

This is essentially impossible on the forest floor in the tropics

Abandon dead wood
Develop separate piece nests
Allow habitat and trophic expansion
Now have to forage and to build

OBLIGATE EUSOCIALITY



Sterile worker castes
Centrally provisioned nests
Energetics of helping

Energetic costs of helpers (to colony)

- Dead-wood-nesting helpers:
 - rearing costs only, may be minimal (Korb)
- Central nesting helpers:
 - rearing costs
 - *plus*, nest/mound building and nest/mound maintenance costs
 - *plus*, foraging costs
- May not be able to ‘afford’ to expend energy on ‘worker reproduction’

Sperm

- Good indicator of monogamy (sperm competition), so gives a pointer to the evolution of eusociality
 1. *Mastotermes* – multiflagellate sperm (very odd)
 2. Termopsids and Kalotermitids – vaguely motile, non flagellate
 3. Rhinotermitids and Termitids – amotile amorphous sperm, no acrosomes
- *Again, correlates perfectly with worker eusociality evolution*

Conclusions (1)

- Ancestor of termites and *Cryocercus* has necessary conditions for eusocial evolution
 - Overlapping generations (dead wood)
 - Brood care (flagellates)
 - Monogamy
- Subsequent evolution dependent on colony expansion, colony interactions and moving to central (separate piece) and colony location strategy

Conclusions (2)

- Soldier evolution and worker evolution are decoupled, as defence and helping are not logically or biologically connected
- There is no single origin of 'eusociality' in termites
 - defence line (soldiers)
 - helping line (workers)
- This is completely different from Hymenoptera

And now...

Splurge...