BioOne COMPLETE

The nest architecture of the ant, Camponotus socius

Author: Tschinkel, Walter R.

Source: Journal of Insect Science, 5(9) : 1-18

Published By: Entomological Society of America

URL: https://doi.org/10.1673/031.005.0901

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Tschinkel WR. 2005. The nest architecture of the ant, *Camponotus socius*. 18pp. *Journal of Insect Science*, 5:9, Available online: insectscience.org/5.9

Journal of Insect Science

insectscience.org

The nest architecture of the ant, *Camponotus socius*

Walter R. Tschinkel

Department of Biological Science, Florida State University, Tallahassee, Florida 32306–4370 U.S.A.
tschinkel@bio.fsu.edu

Received 2 July 2004, Accepted 11 12 2004, Published 4 April 2005

Abstract

The architecture of subterranean nests of the ant *Camponotus socius* was studied from casts of plaster or metal. Twenty-four such casts are illustrated using stereo pairs of images. After study, plaster casts were dissolved to retrieve the workers embedded in them, providing a census of the ants that excavated the nest. Nests were up to 60 cm deep, and were composed of descending shafts connecting up to about 10 horizontal chambers. Nest volume ranged up to almost 800 cm^3 and total chamber area up to almost 500 cm^2. Both volume and area were closely and positively related to the number of workers in the nest. Nest enlargement occurred through the simultaneous enlargement of chambers, deepening of the nest and addition of more chambers. Chamber enlargement contributed most to nest growth. Chambers near the surface were elongate and tunnel-like, while deeper chambers were more compact in outline. As chambers were enlarged, their outlines became more complex and lobed. Workers were polymorphic with clearly distinguishable minor and major workers. The headwidth of minors averaged 1.45 to 1.65 mm, and that of majors 2.30 to 2.80 mm. The mean headwidth of minors increased significantly as the proportion of major workers increased, but the trend of major headwidths fell short of significance. The numerical proportion of majors ranged from 3% to 38% and averaged 15% of the workers, while their biomass proportion ranged from 10% to 75%, averaging about 50%. The queen was recovered in 6 of the 14 plaster nests, suggesting that the average colony of this polydomous species has 2.3 nests. Because of the lateness of the season when casts were made (October), only two nests contained significant amounts of brood. The possible functional roles of nest architecture in ants are discussed.

Keywords: chambers, colony size, headwidth, nest structure, polydomous, worker polymorphism, worker size

Introduction

The architecture of subterranean ant nests has rarely been subjected to careful, quantitative study, and is largely *subterra incognita*. Unlike the well-studied nests of wasps and bees, those of ants are produced by soil removal rather than construction, and are probably based on different behavioral programs. Most reports provide only simple verbal descriptions or simple drawings based on excavations, and very few included a census of the colony or quantitative details of the architecture. This literature is reviewed in Tschinkel (2005). In spite of these shortcomings, it is clear that ants excavate species-typical subterranean nests, a conclusion strengthened by the more recent work of Tschinkel (1987, 1999a, 1999b, 2003, 2005), Mikheyev and Tschinkel (2005) and Moreira *et al*. (2004). Although perhaps not universal, many ant nests consist of two basic elements: more or less vertical shafts and more or less horizontal chambers. Variation in the shape, size, number and arrangement of these basic elements gives rise to species-typical architecture. Examples of several species can be found in Tschinkel (2003, 2005).

The connection between nest architecture and colony function has received little attention. Brian (1956) showed that ants in smaller groups rear brood more efficiently than those in larger groups, a result confirmed by Porter and Tschinkel (1985). Nest architecture combines with the tendency of all ants to sort themselves and their brood to produce social structure within the nest. In most species, workers move centrifugally away from the brood as they (the workers) age (Hölldobler and Wilson 1990; Sendova Franks and Franks 1995), a movement that is connected to age polyethism. In deep nests such as those of the Florida harvester ant, *Pogonomyrmex badius*, this movement sorts workers by age such that the youngest are located mostly in the bottom third of the nest and the oldest (defenders and foragers) near and on the surface (Tschinkel 1999a). Considering the near universality of the centrifugal movement of aging workers away from the brood pile, it seems likely that nest architecture and spatial social structure are functional and contribute to colony fitness. Determining whether these links exist and how they function should be a central question in the study of ant nest architecture.

However, before these questions can be addressed, it is necessary to describe, in quantitative terms, the structure and range of variation of the nests of a variety of ant species, as well as the distribution of the ants within these structures. This paper provides a description of the nest architecture and its variation for the ant, *Camponotus socius,* and together with several previous papers (Tschinkel 1987, 1999a, 2003, 2005; Mikheyev and Tschinkel 2004)

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

and some older reports (Dlussky 1981; Darlington 1997; Conway 1983; Kondoh 1968; Lavigne 1969), represents the beginnings of a systematic study of ant nest architecture for its own sake.

Materials and Methods

Study sites

Camponotus socius is the largest-bodied ant of the Florida coastal plain, occurring primarily in the so-called sandhills ecotype. This is primarily longleaf pine/wiregrass forest developed on excessively drained sands derived from old beach dunes. Relief is moderate, usually not exceeding 20 m between hilltops and the occasional wetlands in depressions and sinkholes. The nests in this study were located in a longleaf pine/wiregrass/turkey oak area about 10 km southwest of Tallahassee, Florida in the Apalachicola National Forest. Other common ants at the same site included *Forelius pruinosus, Trachymyrmex septentrionalis, Aphaenogaster floridanus, Aphaenogaster treatae, Camponotus floridanus, Pogonomyrmex badius, Solenopsis geminata*, and *Pheidole morrissi*.

Nest casting

Two casting methods were used to render the architecture visible. Fourteen nests were cast with orthodontal plaster, a method first published by Williams and Lofgren (1988). A thin slurry of this plaster in water was simply poured into the nest entrance until the nest was filled. After about an hour, the hardened cast was excavated, taken to the laboratory and dried. Casts always broke upon excavation and were therefore reconstructed with 5-minute epoxy glue after the pieces had dried.

An additional 10 casts were made using molten zinc or aluminum. The metals were melted in a portable, charcoal-fired kiln provided with a draft from a car heater fan run on a battery. The bottom of a scuba tank served as a crucible. More details can be found in Tschinkel (2005). In contrast to the fragile plaster casts, metal casts of *C. socius* nests were very strong and never broke, and were effective weapons in barroom fights.

Both the reconstructed plaster and the metal nests were photographed as stereo pairs from a standard vantage point, with a scale. These images are provided below. Most nest measurements were taken from the scaled digital photos of the plaster nests, but plaster nests were also weighed to allow an estimate of total volume from the density of dry plaster. The complete casts were photographed and then broken; the chambers were laid flat and photographed from directly above, with a scale. Chamber areas and shapes were determined from these photographs.

Finally, the pieces of each plaster cast were enclosed in a fine-mesh bag and placed in the seawater outflow of the Florida State University Marine Laboratory. Over about a month, the plaster slowly dissolved leaving behind the ants that had been entombed in the cast. These were counted to provide a census of the ants that built each nest. The heads were separated for headwidth measurement using a Porter wedge-micrometer (Porter 1983), providing an estimate of worker size and size distribution.

It is not possible to derive a census from metal casts (although tiny, charred carcasses were often visible), so these casts provide only structural information without information about the colony that built the nest.

Data were analyzed by ANOVA and multiple regressions, and were transformed to stabilize the variance as necessary.

Results

Representative casts of *C. socius* nests are shown as stereo pair digital photographs in Figs. 1–7. Each nest cast is shown from opposite vantages that together allow the viewer to experience a fairly complete 3-dimensional image. Images can be printed, separated and viewed with a stereo viewer. Stereo images of all remaining nest casts are shown in Appendices 1–13. Appendices 14–17 are not stereo images, the casts having been disposed of before the stereo idea occurred to me.

Nests of *C. socius* consist of 2 to 10 chambers arranged along a shaft that descends at an angle from 45 to almost 90 degrees from the horizontal. Angles were lower near the surface than at depth. Horizontal-floored or mildly inclined chambers intersected

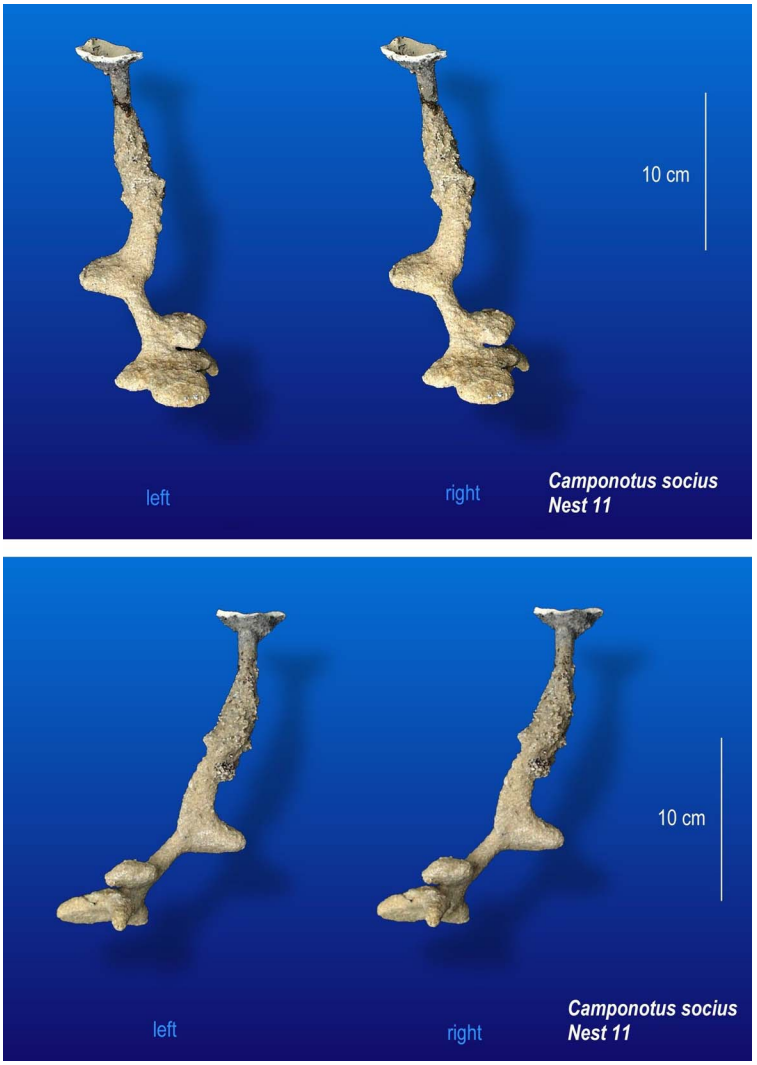


Figure 1. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

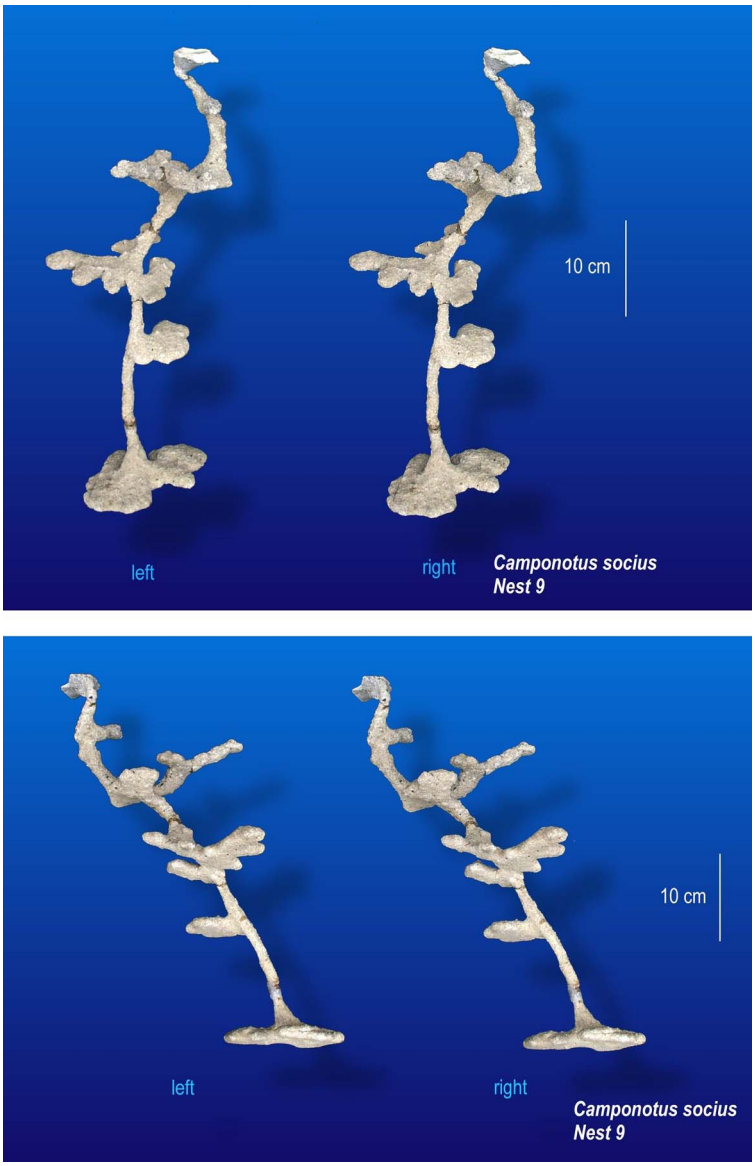


Figure 2. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

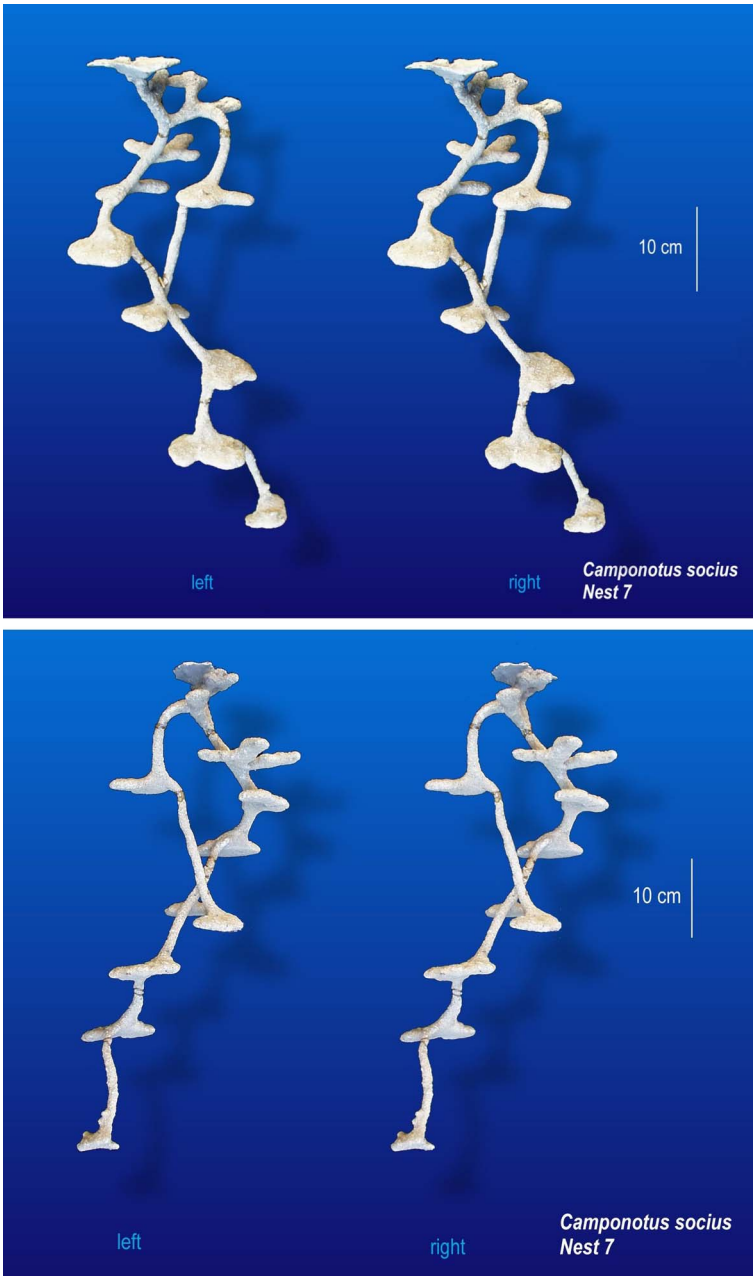


Figure 3. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

this shaft. Chamber height was usually between 1.0 and 1.5 cm, typically thinner at the outer edges than at the connection to the shaft. In 5 of 24 cases, nests contained 2 shafts, but none contained more. Shaft branching always occurred in the upper parts of larger nests.

Size-related architectural patterns

Figure 8 shows 13 of the plaster casts all to the same scale, revealing their relative sizes. It is likely that these nests also represent approximate ontogenetic stages of nest growth. The dissolution of these plaster casts to retrieve the workers entombed within them showed that the total nest volume or chamber area was strongly related to the number of workers within the nest (Fig. 9). The number of workers ranged from 2 to 590, and accounted for 84% of the variation in total chamber area (regression: $A = 0.70W + 67.9$; $t_{12} = 8.20$; $p < 0.00001$). Total chamber area varied from 26 to 467 cm^2. Every additional worker increased chamber area by 0.70 cm^2 (slope of the regression). Results were very similar with total nest volume, which ranged from 70 to 765 cm^3.

The increase in total chamber area resulted from the

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

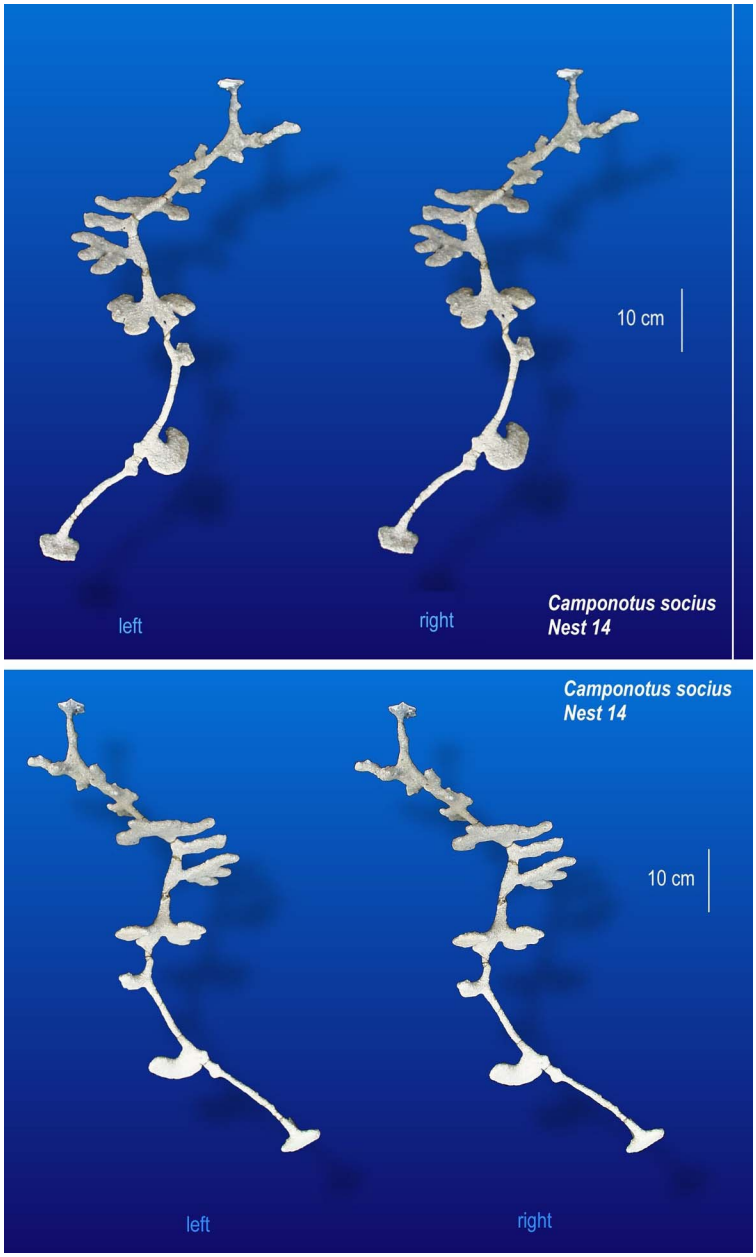


Figure 4. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

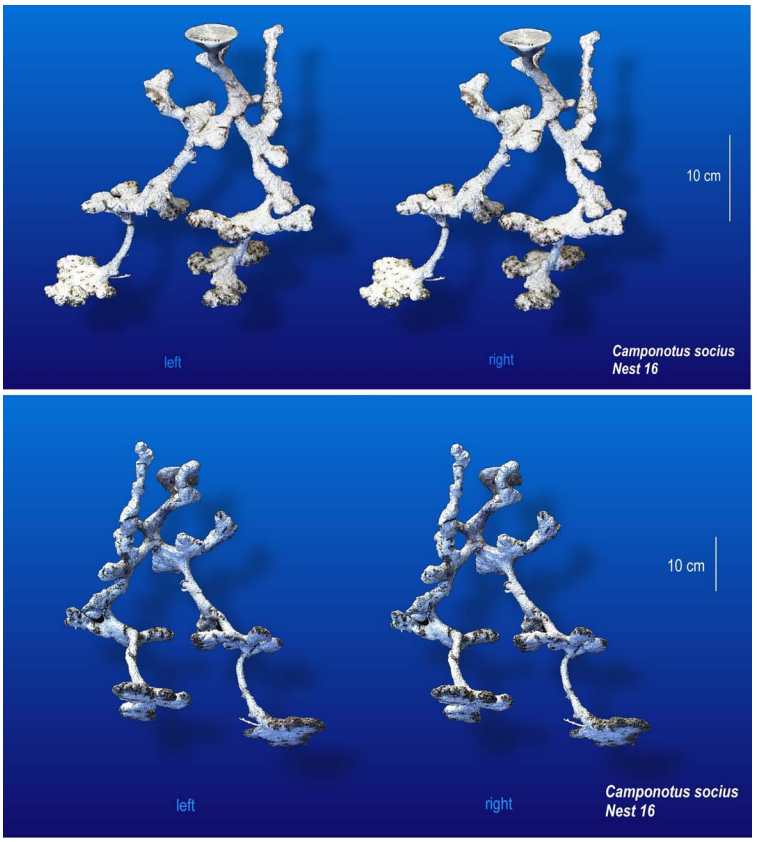


Figure 5. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

simultaneous increase in the number and size (mean area) of chambers (Fig. 10). As nests increased in size, the number of chambers increased from 2 to 10, and their mean area from 13 to 47 cm^2. Nest depth also increased with total nest size (Fig. 11), from 15 to 66 cm, and when entered together with the log mean chamber area, explained 95% of the variance in log total area. The partial correlation was 0.57 for nest depth and 0.94 for log mean chamber area, indicating that the total nest area depended more strongly on the size of the chambers than the depth of the nest. Number of chambers alone explained 82% of the variance in total area, with nest depth adding nothing further to the explained variance. The combination of increasing nest depth and addition of more chambers assured that the spacing between chambers increased only slightly with depth (Fig. 12), from a mean of about 4 to about 6.5 cm. Because of high variability, chamber depth accounted for only about 27% of the variation in spacing between chambers (regression: $S = 0.11D + 2.95$; $t_{69} = 5.30$; $p < 0.00001$).

Chamber shape

Chambers differed in shape (horizontal outline) depending on their size and vertical location. Chambers near the surface tended to be narrower and more linear, resembling shafts, whereas deeper chambers tended to be more compact in outline. Thus, the ratio of the chamber width to length was lower in near-surface chambers than deeper chambers (Fig. 13), but this was expressed primarily in larger nests with more than 200 cm^2 total area and 20 cm maximum depth. The shaft-like upper chambers often angled upward to just beneath the soil surface, but never broke through. These upper chambers may be created by a different behavioral program than the deeper ones. Chamber height did not vary significantly with chamber area or total area.

As chambers increased in size, their outline changed from

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

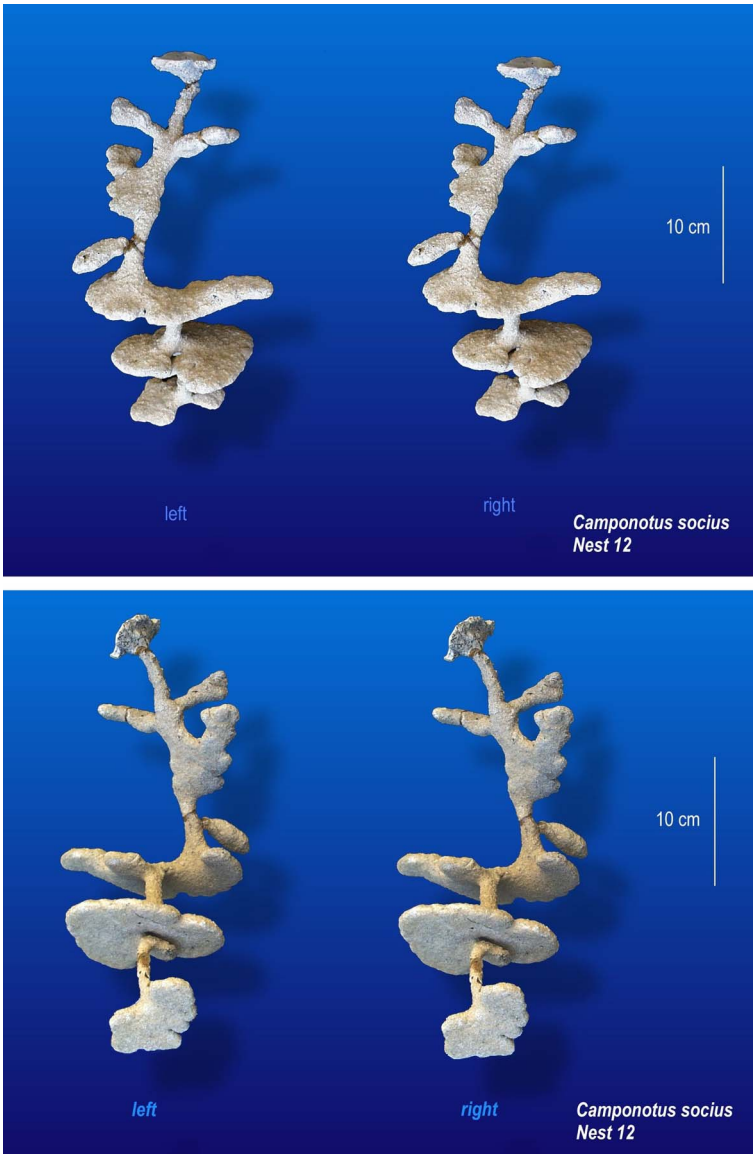


Figure 6. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

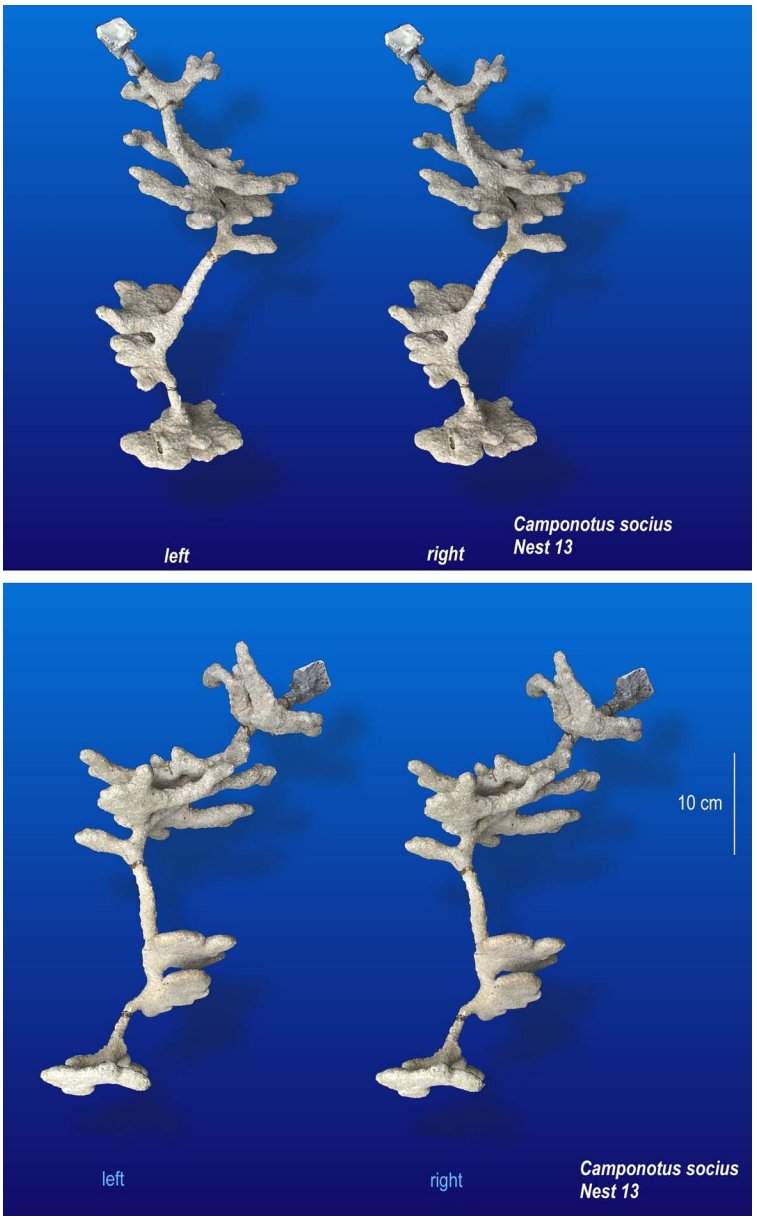


Figure 7. Representative casts of the nests of *Camponotus socius*, chosen to show the range of size and structure. Each nest is shown as two stereo pairs, each from an opposing vantage point. Proper ocular technique or a stereo viewer will render these images in 3-D.

simple to complex and lobed, increasing the ratio of the perimeter to the area. The ratio of the actual perimeter to the perimeter of an equal-area circle (the minimum possible perimeter) is shown in Fig. 14, along with examples of small and large chambers. Chamber area accounted for 80% of the variation of this ratio (regression of log ratio (y) vs. square root of area (x): $y = 0.035 + 0.0057x$; $t_{81} = 18.1$; $p < 0.000001$). Addition of the number of chamber lobes (defined as outline deviations longer than their width at the base) raised the explained variance to 83%, showing that lobes are somewhat redundant with chamber area. Chamber area affected the ratio more strongly than the number of lobes (partial correlations, 81 vs. 37%, respectively). Only the largest chambers had multiple lobes (Fig. 14).

Workers

Worker headwidths were used as a measure of worker size. Worker size distributions were clearly bimodal. Minors had headwidths ranging from 1.2 to 2.0 mm, and majors from 2.2 to 3.2 mm. The few workers with headwidth of 2.0 to 2.2 mm could not be easily assigned to the major or minor categories, and were divided evenly between them for calculating mean headwidths. Mean headwidths (by nest) for major workers varied from 2.3 to 2.8 mm, and for minor workers from 1.45 to 1.65 mm (Fig. 15). The mean size of minor workers increased about 14% as the proportion

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

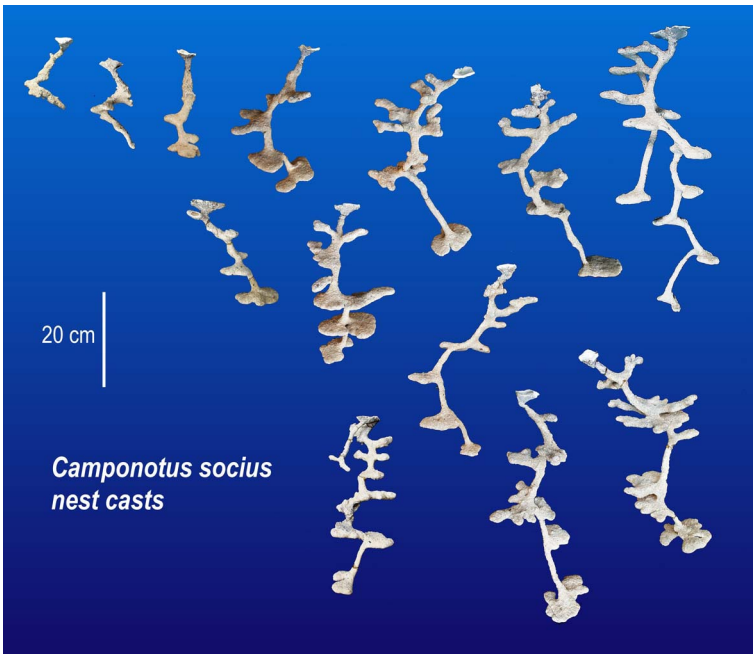


Figure 8. All plaster casts shown to the same scale. Seen from left to right, these approximately represent the progress of nest growth. Note the increase in nest depth, number and size of chambers, and the occasional occurrence of two shafts.

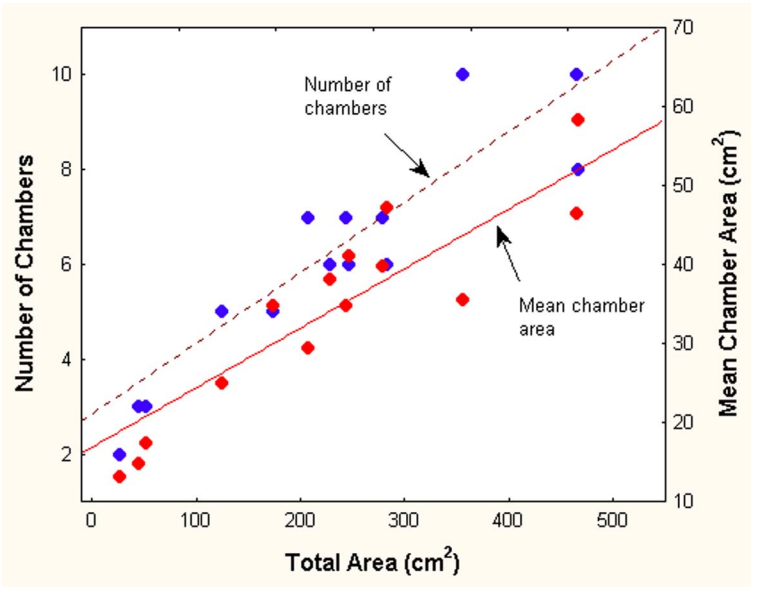


Figure 10. Total chamber area increases through the simultaneous enlargement of chambers and the addition of more chambers. Mean chamber area and number of chambers approximately triple across the range of nest sizes.

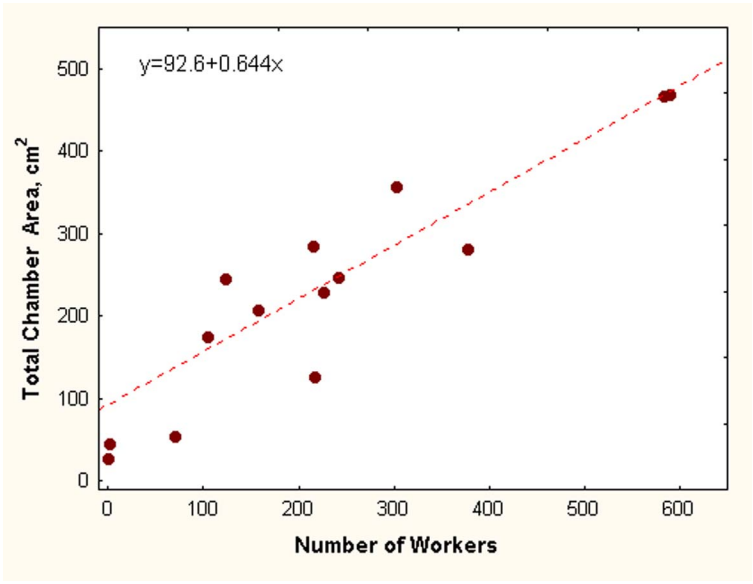


Figure 9. Total chamber area is closely related to the number of workers in the nest, and increases 0.70 cm^2 for each additional worker.

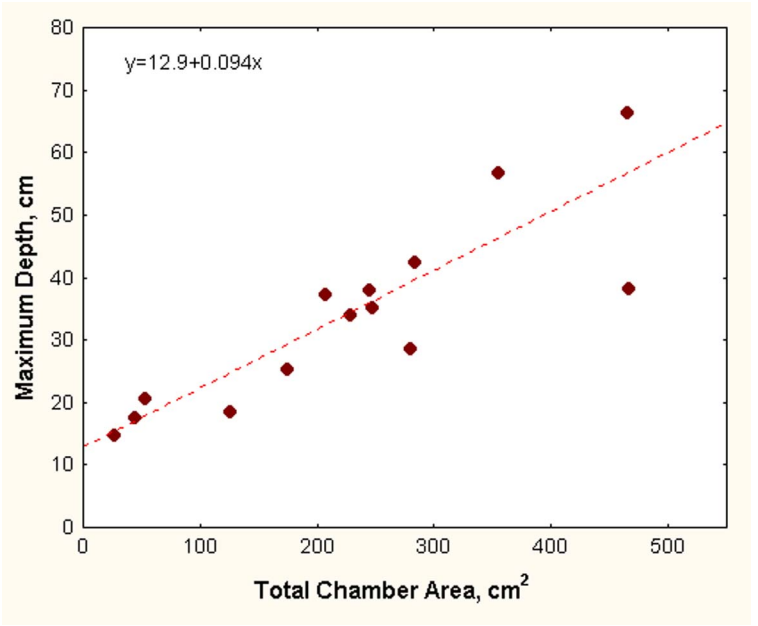


Figure 11. Maximum nest depth increases as total nest size increases. Across an approximately 20-fold increase in total area, nest depth triples.

of majors increased (HW_{min} = 0.005 (% majors) + 1.46; d.f. = 1, 10; R^2 = 51%; $p < 0.01$). Although major headwidth also increased with % majors, this relationship was more variable and not significant. The body weight of majors averaged 6 to 10 times that of minors.

The proportion of major workers varied between 3 and 38% (average 15%), but was not significantly related to the number of workers, although the smallest colony also had the lowest proportion of majors. However, the % majors increased significantly with total nest area (log % majors = 0.83 log total area –0.86; d.f. = 1, 10; R^2 = 48%; $p < 0.01$). It is possible that polydomy obscured the relationship between worker number and % major workers.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

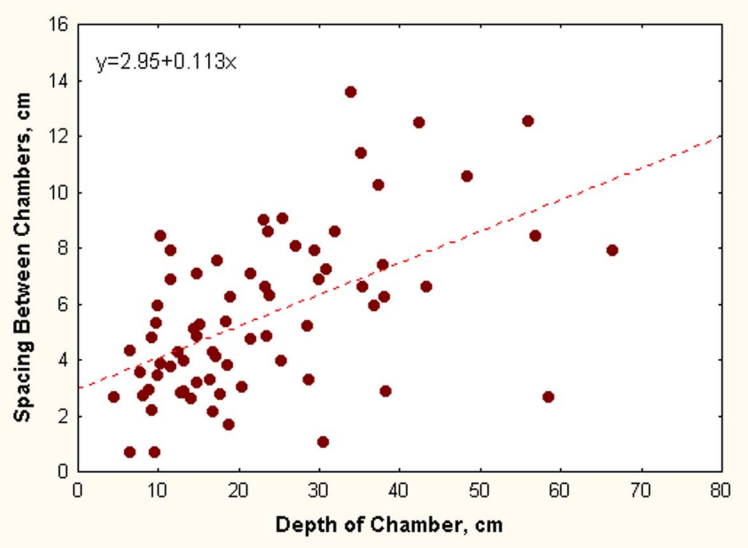


Figure 12. Spacing between sequential chambers increases significantly with chamber depth, but depth only explains 27% of the variance in spacing.

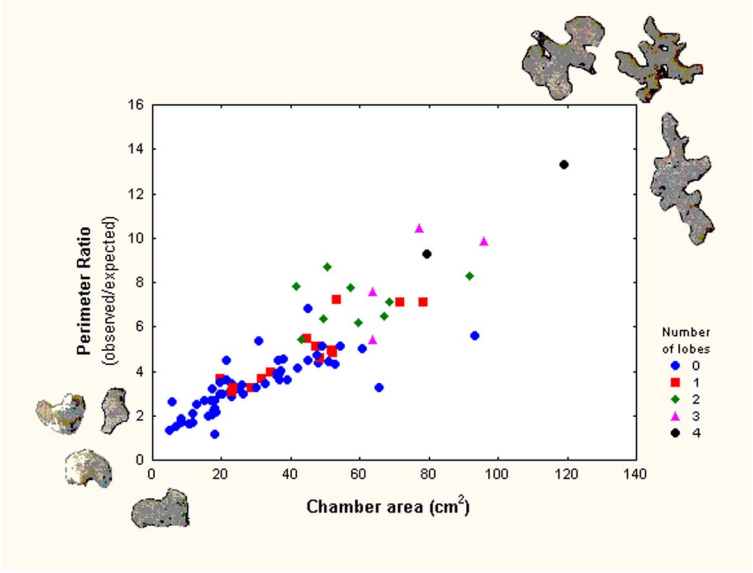


Figure 14. As chambers are enlarged, they become more complex and lobed in outline. This is estimated as the measured chamber perimeter:area ratio to that expected for an equal-area circle. For circular chambers this estimate is 1.0.

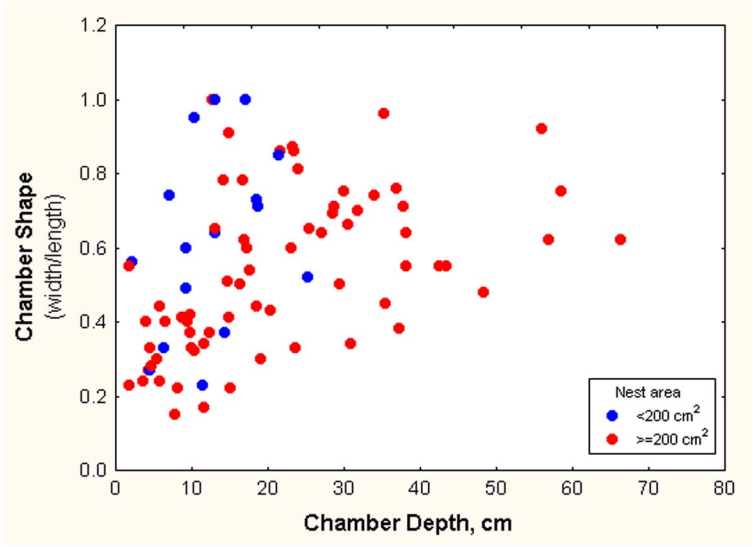


Figure 13. Chamber shape (width/length) changes with chamber depth, becoming less elongate and more compact, but this effect is only seen in larger nests (red symbols).

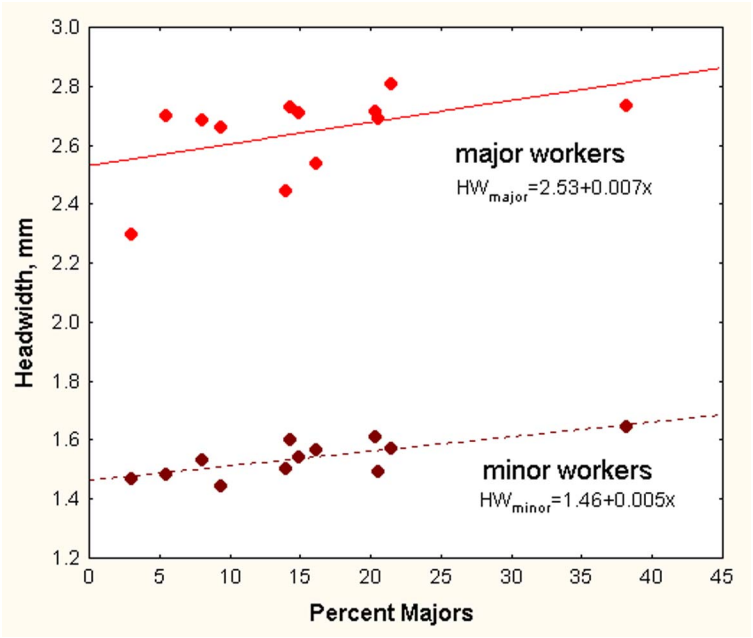


Figure 15. The size of minor workers (headwidth) increases significantly by 14% as the proportion of major workers increases. The increase in the size of majors falls short of significance.

Assuming that the cube of the headwidth is roughly proportional to the worker body weight, the proportion of worker biomass represented by majors ranged from about 10 to 75%, averaging about 50% over all nests.

The queen was recovered from 6 of the 14 plaster casts, suggesting that the average *C. socius* colony occupies 2 to 3 nests. There is no possibility that queens were present in the remaining nests, but were missed. This polydomy probably accounts for the clustered occurrence of *C. socius* nests (personal observation).

Several nests contained 1 to 3 cocoons, but one nest of 158 workers contained 38 cocoons, and another of 243 contained 39 cocoons. No evidence of other brood was found, and it was probably absent because of the lateness of the season (October). The cocoons probably represent the last batch of workers produced before winter.

Discussion

Camponotus socius excavates nests with characteristic structure and variation. Nest size is strongly proportional to the

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

population of workers within, which ranges up to 600 workers. At the extreme, depth rarely exceeds 65 cm, total nest area is generally less than 500 cm^2, and chambers number 10 or fewer. Chamber height is more or less invariant, but chamber shape becomes more complex and lobed in characteristic ways as chambers are enlarged. Chambers near the surface are more tunnel-like whereas deeper ones are more compact. The shaft connecting these chambers is usually less than vertical in inclination, and wanders in a vaguely zig-zag or helical manner. The majority of nests have a single shaft, but larger nests may have two as a result of branching near the surface. The vertical separation between chambers varies between 2 and 14 cm and increases slightly with depth. All together, this creates a nest architecture readily attributable to *C. socius*. The species-typical patterns and the tight relationship between the number of workers and nest size imply strong feedback between the nest and the workers.

This architecture shares some characteristics with that of other ant species. Most generally, nests consist of two basic units, approximately horizontal chambers, and descending shafts connecting them (Tschinkel 2003). As in *Pogonomyrmex badius* (Tschinkel 2005), upper chambers are elongate and tunnel-like, contrasting with the more compact chambers below, and chambers become more lobed as they are enlarged. These features are also present in *Prenolepis imparis* (Tschinkel 1987) in which the superficial chambers are anastamosing tunnels separated by about a meter from the more compact deeper chambers (that also become lobed upon enlargement). In most ants, chamber height does not vary with nest or chamber size, probably because it is tailored to the working-height of the ants. More profoundly, the shaft-and-chamber arrangement represents a kind of unit-construction in most ants, with jumps in nest size taking place by the addition of such entire units, as well as by chamber addition and enlargement. Nests of *Pheidole morrissi* and *P. badius* may contain up to 5 such units whose branch points are always near the surface. Extreme examples of nests compiled of multiple shaft-chamber units are those of *Solenopsis invicta* and *S. geminata* (both tens of units), and possibly those of the Argentine ant, *Linepithema humile*, although the last appears more chaotic (unpublished data).

In several ant species, the average worker size increases with colony size (Gray 1973; Markin *et al*. 1973; Tschinkel 1988; Tschinkel 1993; Tschinkel 1998; Tschinkel 1999b). In *S. invicta*, both minors and majors increase in size during the first six months of colony growth, with all subsequent increase in mean worker size coming about through an increase in the proportion of majors. In *P. badius*, minors increase in size throughout colony growth, but there is no clear increase in the size or proportion of majors. In the present case of *C. socius*, minor worker size increased in relation to the proportion of major workers, which was related to at least one measure of colony size, total nest area, although not to nest census. Polydomy may obscure the functional size of the colony, blurring relationships to colony size.

Census by solution of the plaster cast was first used by Mikheyev and Tschinkel (2003), and should have general application for any ground nesting ant species. As with most census methods, it does not include foragers that were away from the nest at the time of casting. The *C. socius* nests were cast at midday during a season when most foraging was probably nocturnal, making it likely that most workers were captured in the casts. Other casting materials, such as metal or cement (Moreira *et al*. 2004) do not allow retrieval of workers for census, although they make casts of superior strength.

Camponotus socius nests in the Tampa, Florida area were reported to be polydomous by Hölldobler (1971). The presence of a queen in only a fraction of the nest casts confirms this condition for the study population, and suggests that the average colony has 2.3 nests. As a result, the censuses reported here do not represent entire colonies. Total colony census would be possible by casting all the nests linked by active trails.

It is unknown whether the *C. socius* colony has a vertical social structure by worker age, as occurs in *P. badius* (Tschinkel 1999a), *Pr. imparis* (Tschinkel 1987) and *Camponotus japonicus* (Kondoh 1968) as chamber contents were not individually analyzed. However, differences in chamber shape and size in relation to depth are present, implying that the workers have a cue as to depth. Tschinkel (2005) suggested that a soil gradient in carbon dioxide concentration could serve as a template for depth in *P. badius*. Such gradients probably exist in all soils as a result of micro-organismal metabolism combined with diffusion to the atmosphere, and would be available as a source of depth information to all soil-nesting ants. *Atta vollenweideri* have been shown to possess the sensory capacity to discriminate concentrations of carbon dioxide (Kleineidam and Tautz 1996). These ants construct special oriented turrets on top of the nest mound. These turrets ventilate the nests and reduce the high concentrations of carbon dioxide produced by the fungus gardens deep in the nest (Kleineidam *et al*. 2001).

Although description is a necessary first step, ultimately understanding nest architecture requires a great deal more, including whether and how particular architectures contribute to colony fitness, and the mechanisms of that contribution. It will also require an understanding of how the colony creates species-typical complex nests in the dark, without plan or leader, in other words, how the architecture emerges from the interaction of workers with the environment, the growing nest and each other. Finally, it will require understanding of how architecture evolves with species and how it adapts to local conditions. None of these goals are close to achievement, although tantalizing tidbits do exist.

Acknowledgements

I am grateful to Kevin Haight for technical help and for assistance with metal casting, and to the Florida State University Marine Laboratory for the use of their seawater outflow to dissolve the plaster nests. This is Paper No. 60 of the Fire Ant Research Team.

References

Brian MV. 1956. Group form and causes of working inefficiency in the ant *Myrmica rubra*. *Physiological Zoology* 29:173–194.

Conway JR. 1983. Nest architecture and population of the honey ant, *Myrmecocystus mexicanus* Wesmael (Formicidae), in Colorado. *Southwestern Naturalist* 28: 21–31.

Darlington JPEC. 1997. Comparison of nest structure and caste parameters of sympatric species of *Odontotermes*

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

(Termitidae, Macrotermitidae) in Kenya. *Insectes Sociaux* 44: 393–408.

Dlussky GM. 1981. *Ants of Deserts*. [In Russian]. Moscow, Nauka.

Gray B. 1973. A morphometric study of worker variation in three Myrmecia species (Hymenoptera: Formicidae). *Insectes Sociaux* 20:323–331.

Hölldobler B. 1971. Recruitment behavior in Camponotus socius (Hym. Formicidae). *Zeitschrift fuer Vergleichende Physiologie* 75:123–142.

Hölldobler B, Wilson EO. 1990. The Ants, 1 ed. Cambridge, MA: Belknap/Harvard Press.

Kleineidam C, Ernst R, Roces F. 2001. Wind induced ventilation of the giant nests of the leafcutting ant, *Atta vollenweideri*. Naturwissenschaften 88:301–305.

Kleineidam C, Tautz J. 1996. Perception of carbon dioxide and other "air-condition" parameters in the leaf cutting ant *Atta cephalotes*. Naturwissenschaften 83:566–568

Kondoh M. 1968. Bioeconomic studies on the colony of an ant species, Formica japonica Motschulsky. 1. Nest structure and seasonal change of the colony members. Japanese Journal of Ecology 18:124–133.

Lavigne RJ. 1969. Bionomics and nest structure of *Pogonomyrmex occidentalis* (Hymenoptera: Formicidae). *Annals of the Entomological Society of America* 62: 1166–75.

Markin GP, Dillier JH, Collins HL. 1973. Growth and development of colonies of the red imported fire ant, *Solenopsis invicta*. Annals of the Entomological Society of America 66:803–808.

Mikheyev A, Tschinkel WR. 2004. Nest architecture of the ant Formica pallidefulva: structure, costs and rules of excavation. Insectes Sociaux 51:30–36.

Moreira AA, Forti LC, Boaretto MAC, Andrade APP, Lopes JFS, Ramos VM. 2004. External and internal structure of Atta bisphaerica Forel (Hymenoptera: Formicidae) nests. Journal of Applied Entomology 128:204–211.

Porter SD. 1983. Fast, accurate method of measuring ant headwidths. Annals of the Entomological Society of America. 72:472–484.

Porter SD, Tschinkel WR. 1985. Fire ant polymorphism (Hymenoptera: Formicidae): factors affecting worker size. Annals of the Entomological Society of America 78:381–386.

Sendova Franks AB, Franks NR. 1995. Spatial relationships within nests of the ant Leptothorax unifasciatus (Latr.) and their implications for the division of labour. Animal Behavior 50:121–136.

Tschinkel WR. 1987. Seasonal life history and nest architecture of a winter-active ant, Prenolepis imparis. Insectes Sociaux 34:143–164.

Tschinkel WR. 1988. Colony growth and the ontogeny of worker polymorphism in the fire ant, Solenopsis invicta. Behavioral Ecology and Sociobiology 22:103–115.

Tschinkel WR. 1993. Sociometry and sociogenesis of colonies of the fire ant Solenopsis invicta during one annual cycle. Ecological Monographs 64:425–457.

Tschinkel WR. 1998. Sociometry and sociogenesis of colonies of the harvester ant, Pogonomyrmex badius: worker characteristics in relation to colony size and season. Insectes Sociaux 45:385–410.

Tschinkel WR. 1999a. Sociometry and sociogenesis of colonies of the harvester ant, Pogonomyrmex badius: distribution of workers, brood and seeds within the nest in relation to colony size and season. Ecological Entomology 24:222–237

Tschinkel WR. 1999b. Sociometry and sociogenesis of colony-level attributes of the Florida harvester ant (Hymenoptera : Formicidae). Annals of the Entomological Society of America 92:80–89.

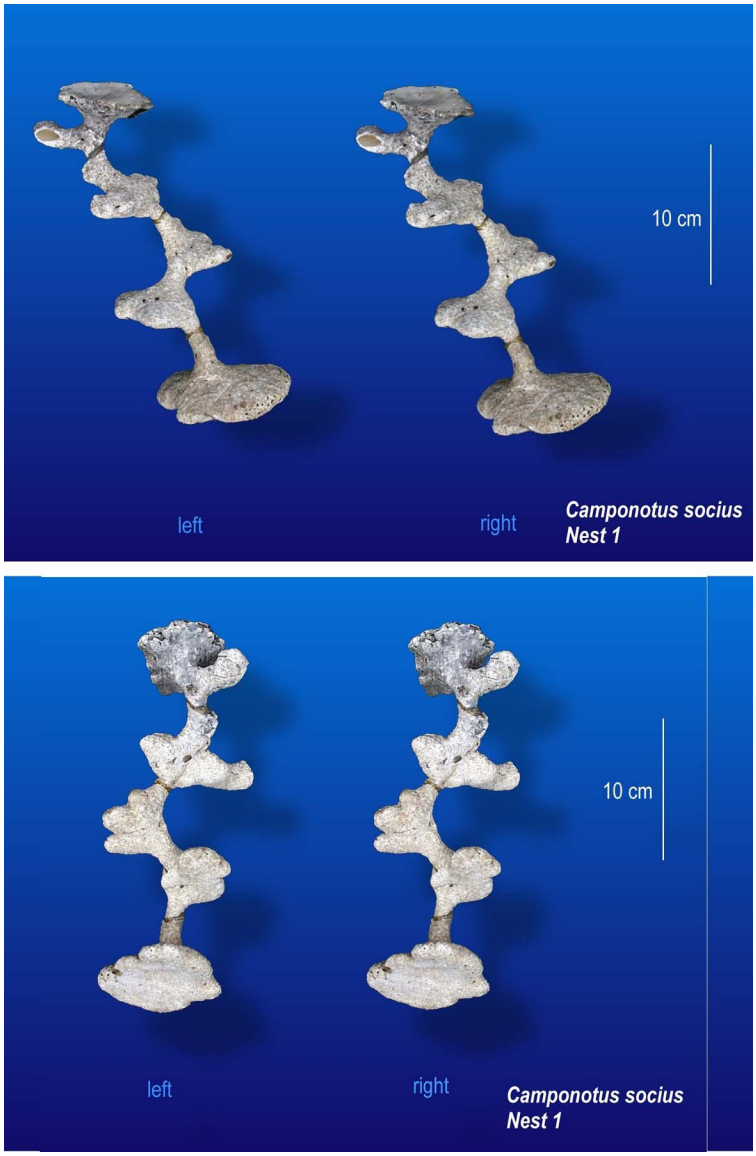
Tschinkel WR. 2003. Subterranean ant nest architecture: trace fossils past and future? Paleogeography Paleoclimatology Paleoecology 192:321–333.

Tschinkel WR. 2005. Nest architecture of the Florida harvester ant, *Pogonomyrmex badius*. *Journal of Insect Science* 5:9.

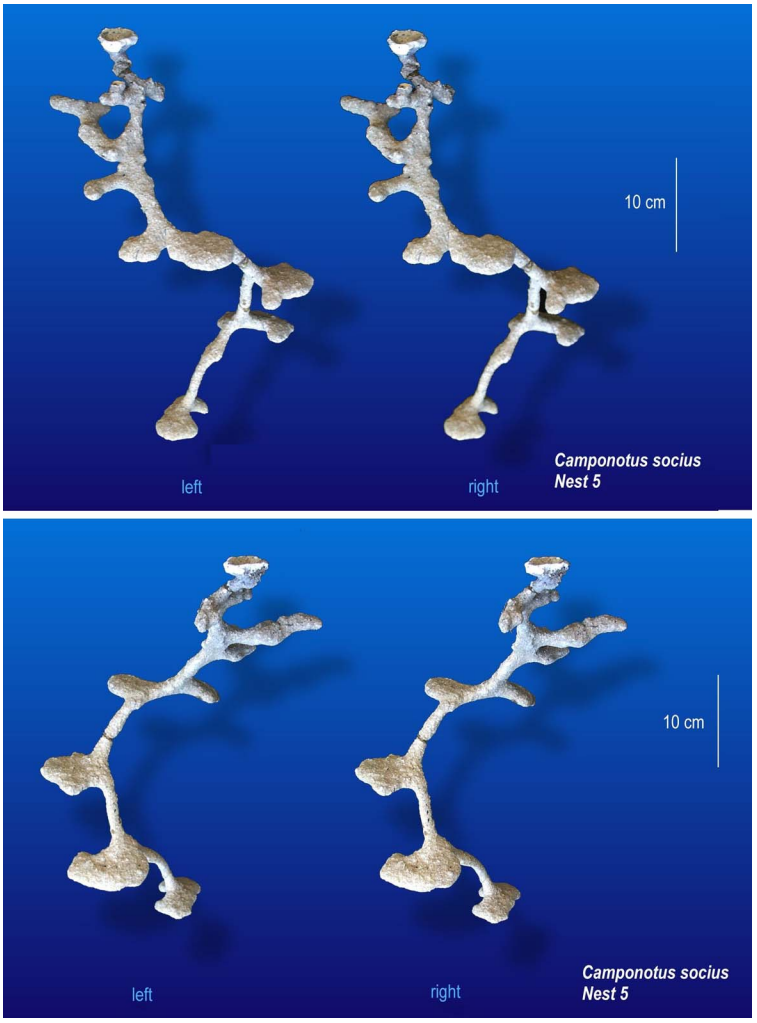
Williams DF, Lofgren CS. 1988. Nest casting of some ground-dwelling Florida ant species using dental labstone. In: *Advances in Myrmecology*. Leiden: E.J. Brill; 433–443.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



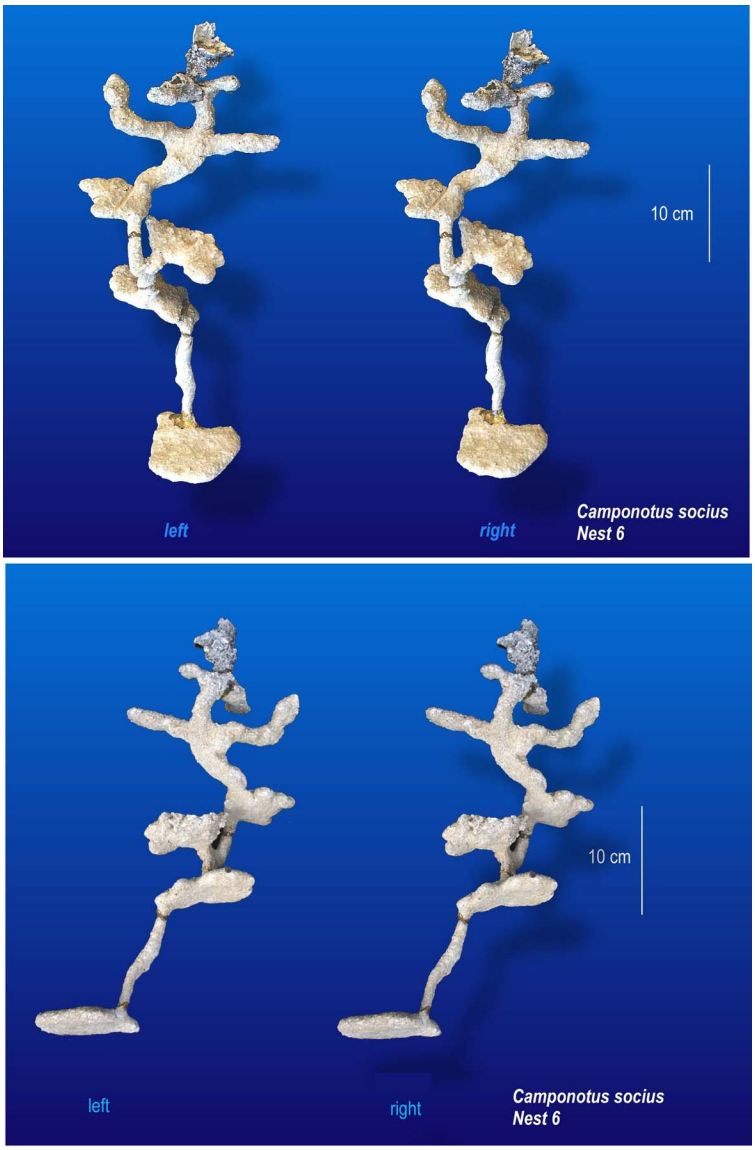
Appendix Figure 1. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.



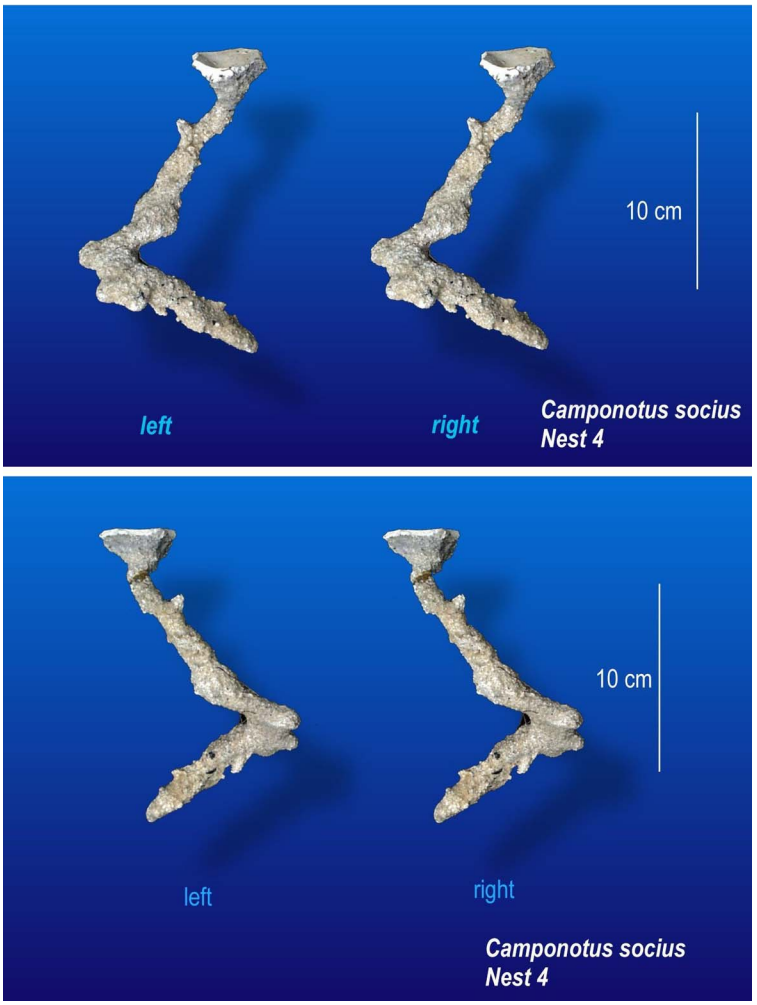
Appendix Figure 2. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



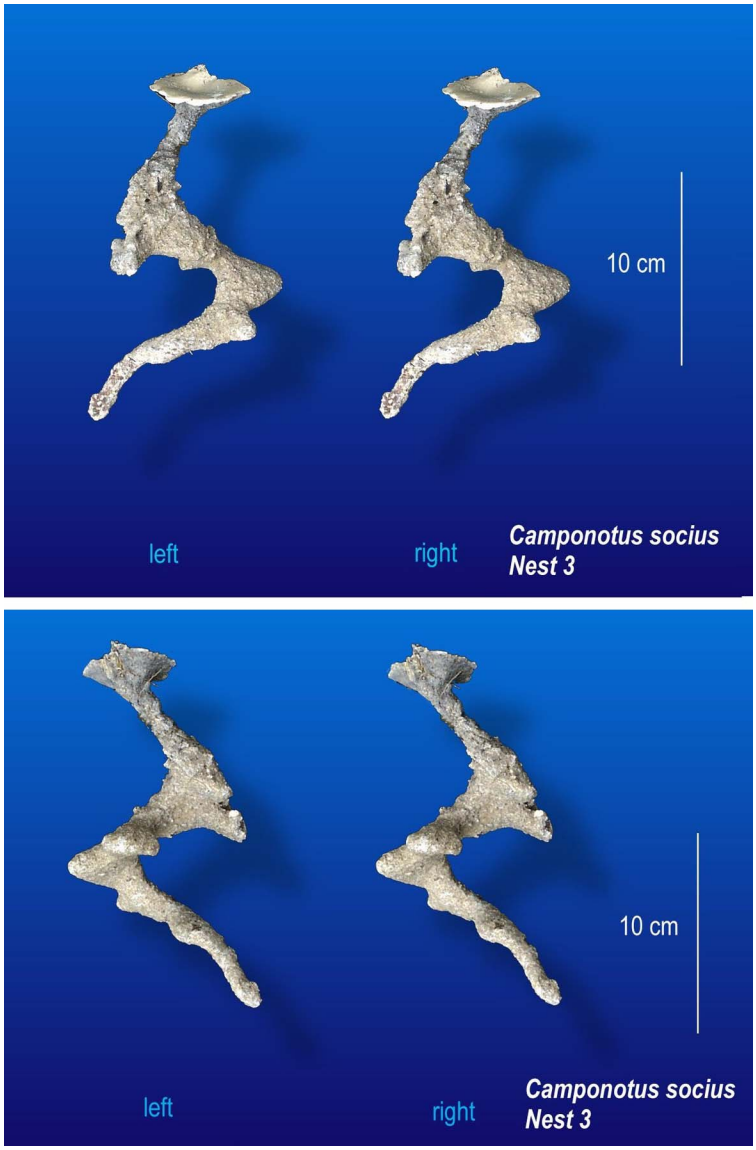
Appendix Figure 3. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.



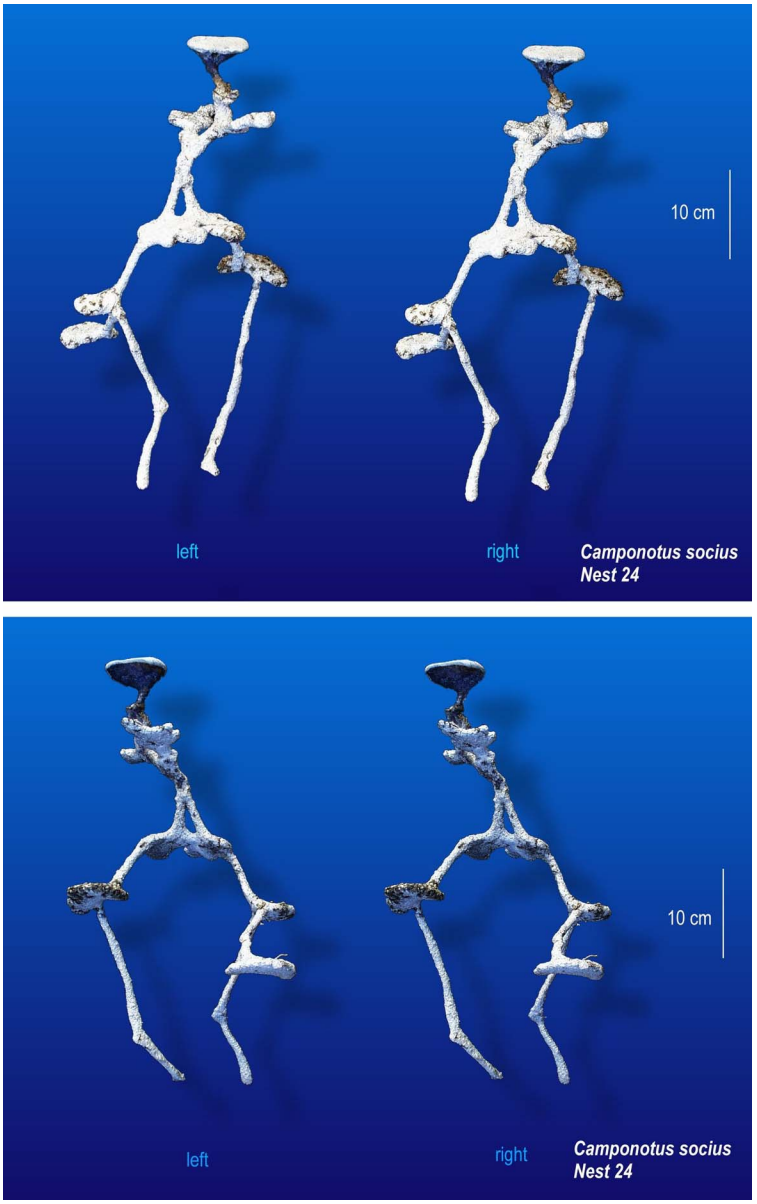
Appendix Figure 4. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



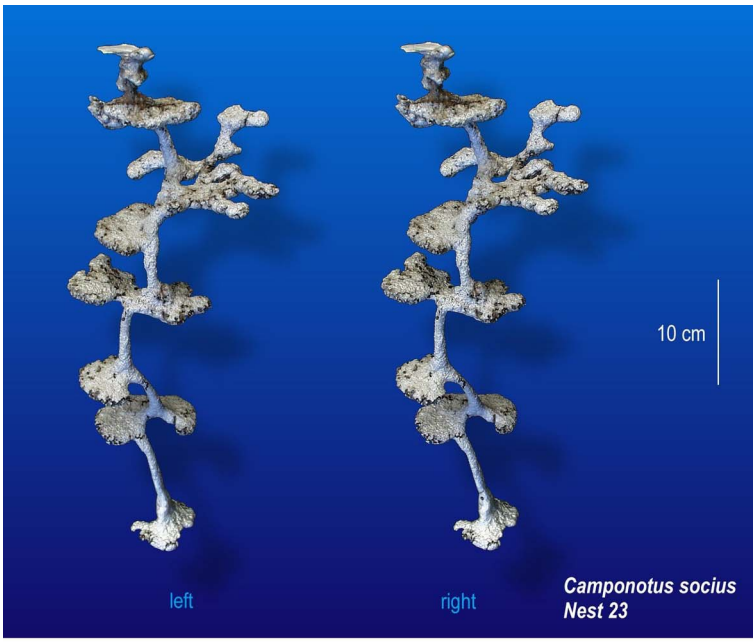
Appendix Figure 5. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

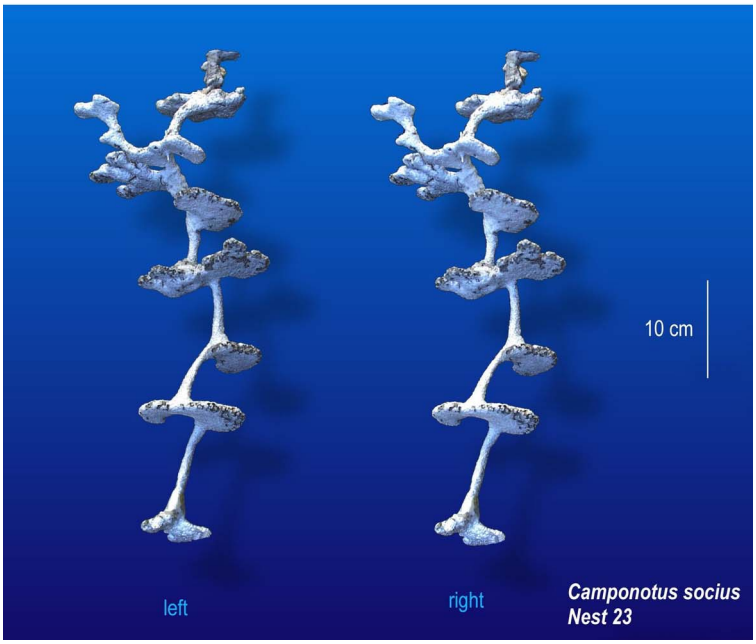


Appendix Figure 6. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

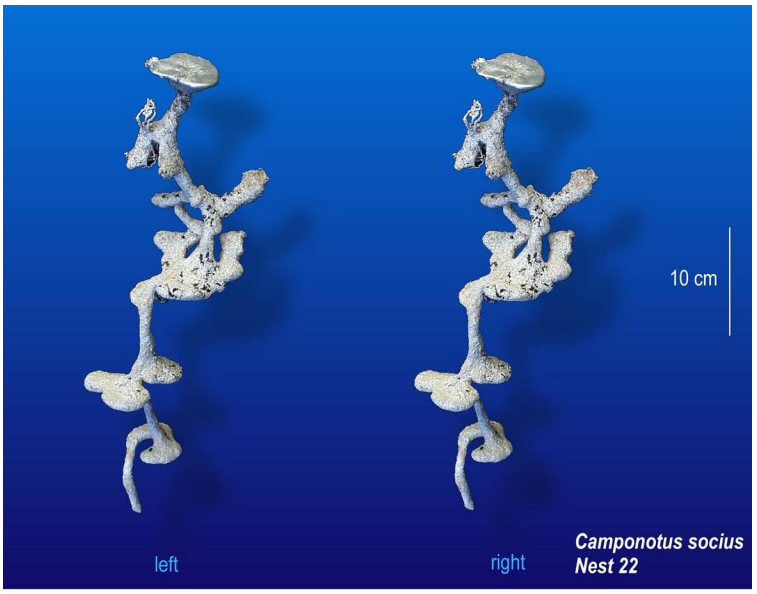
Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

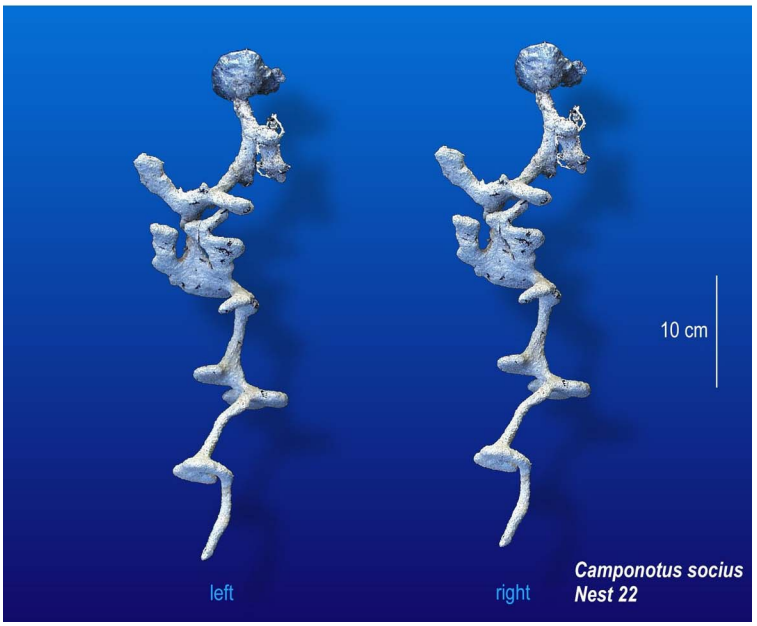
Appendix Figures





Appendix Figure 7. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

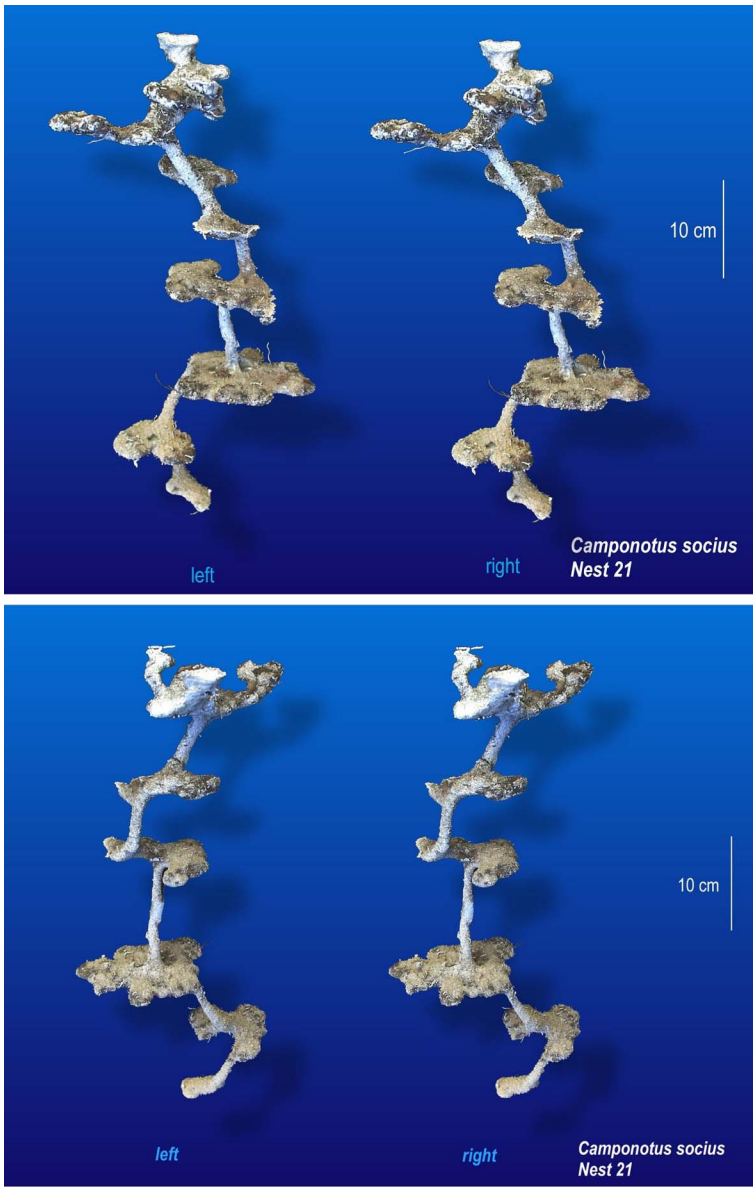




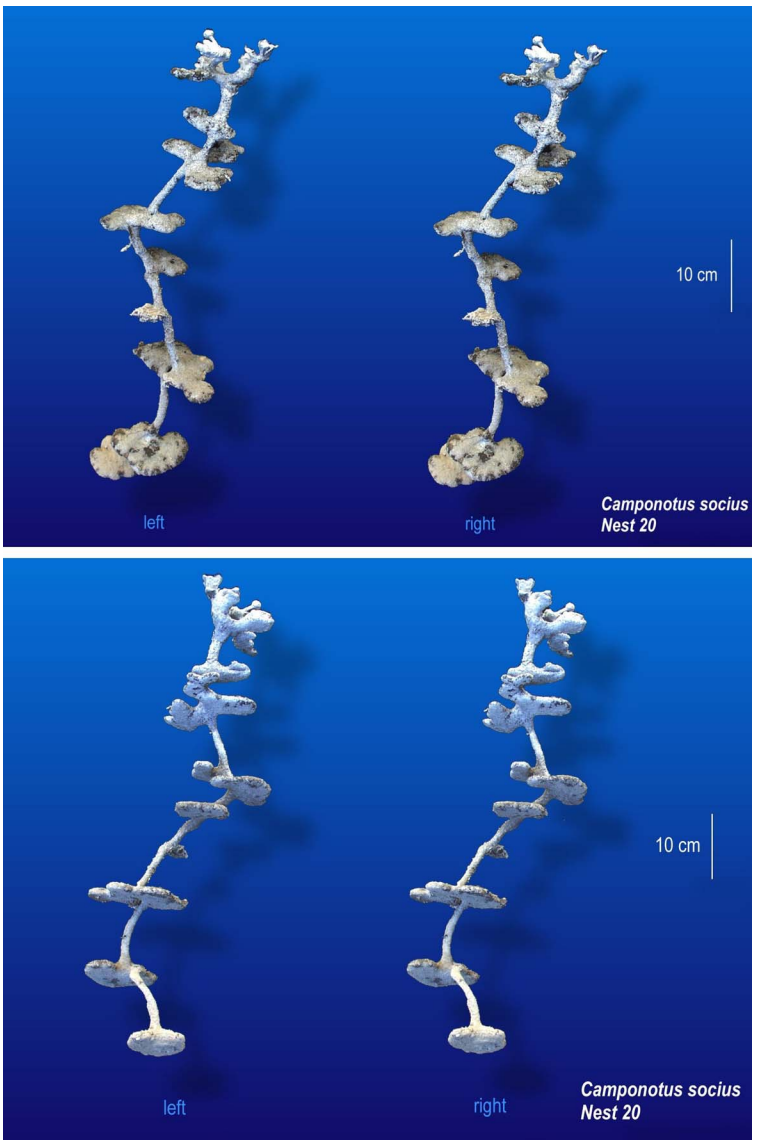
Appendix Figure 8. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



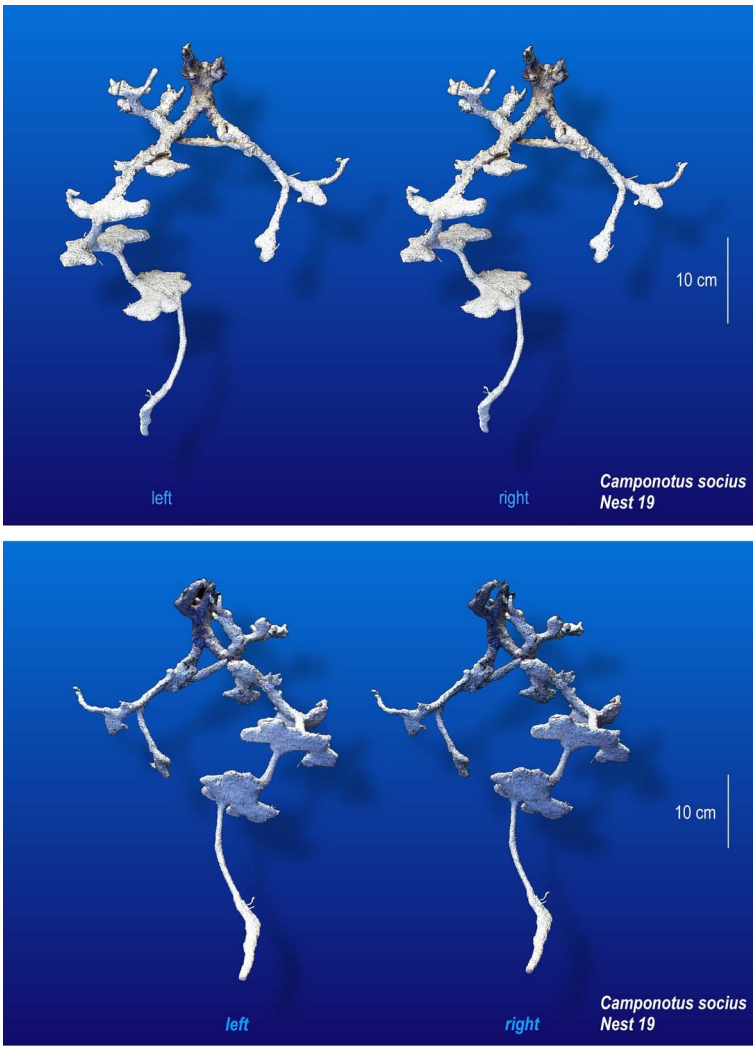
Appendix Figure 9. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.



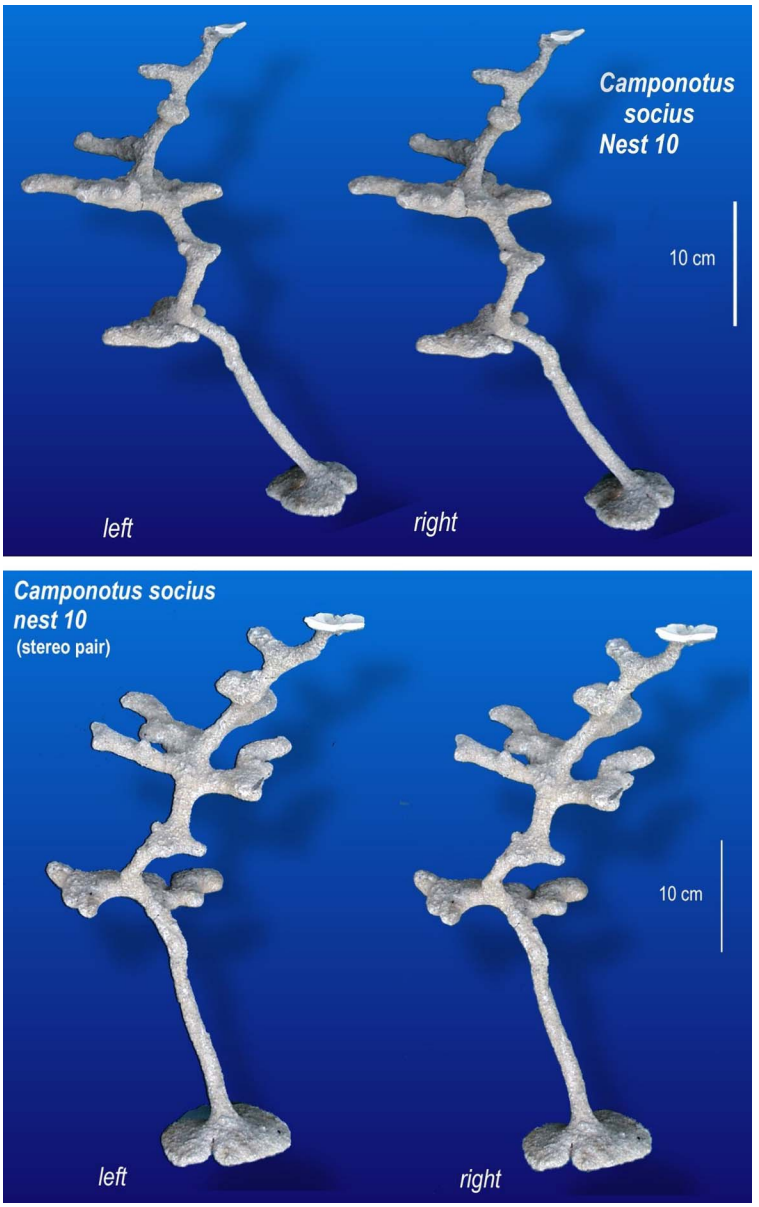
Appendix Figure 10. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



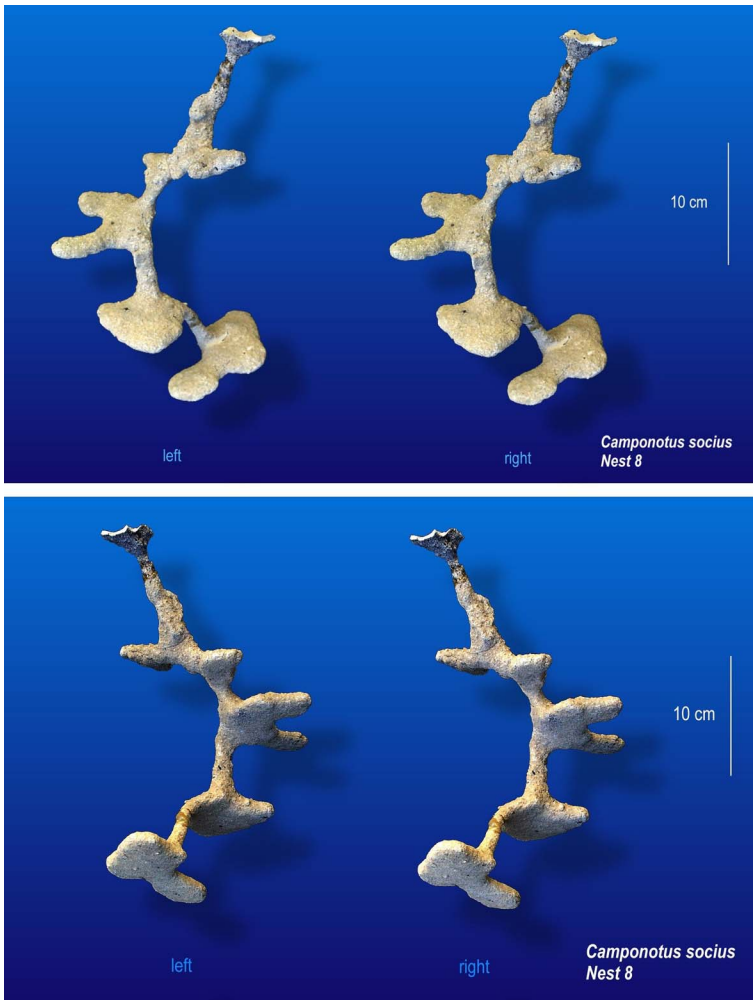
Appendix Figure 11. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.



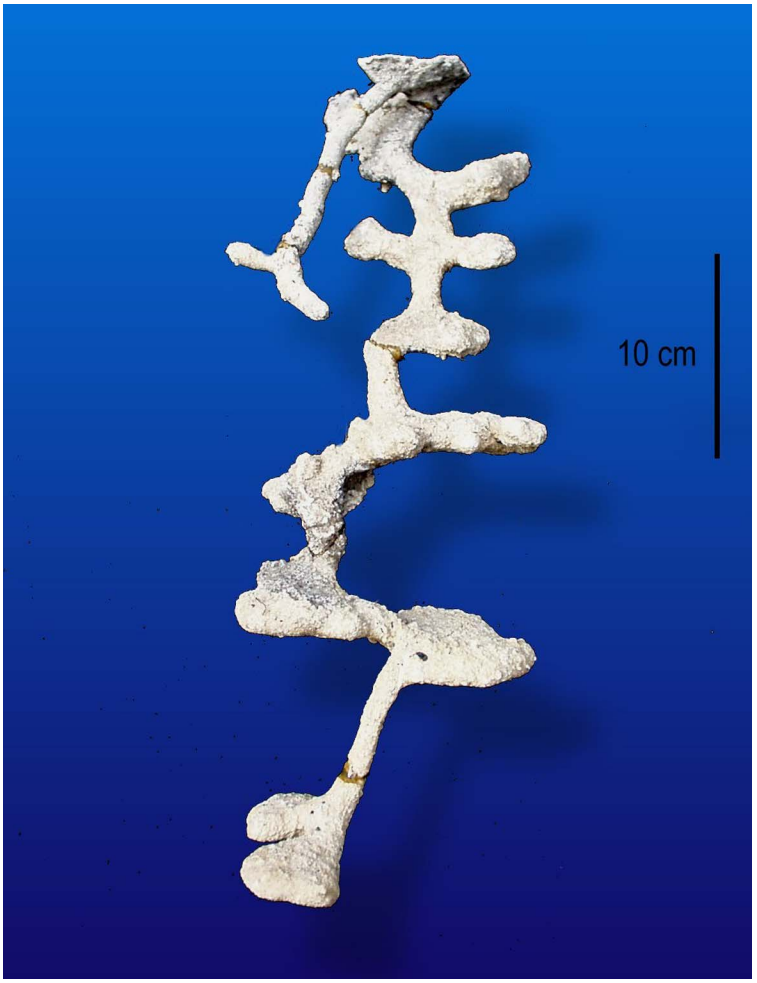
Appendix Figure 12. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



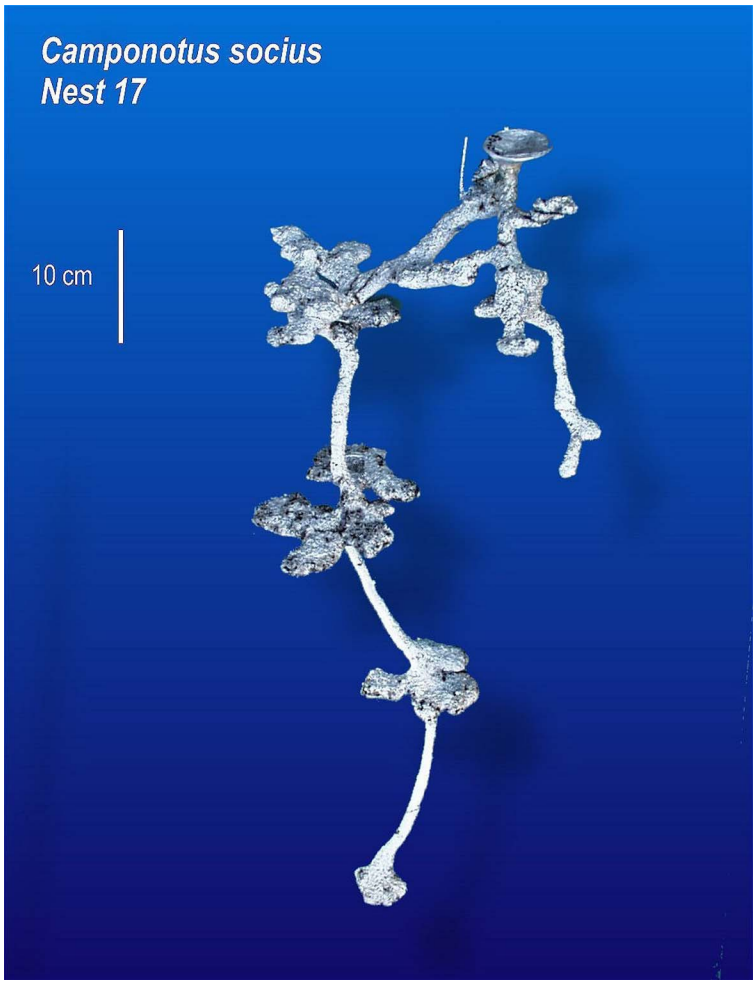
Appendix Figure 13. Stereo pair images of nest casts, taken from opposing vantages. Casts in Appendices 1–5. 12 and 13 are made of orthodontic plaster, those in Appendices 6–11 are aluminum or zinc casts.



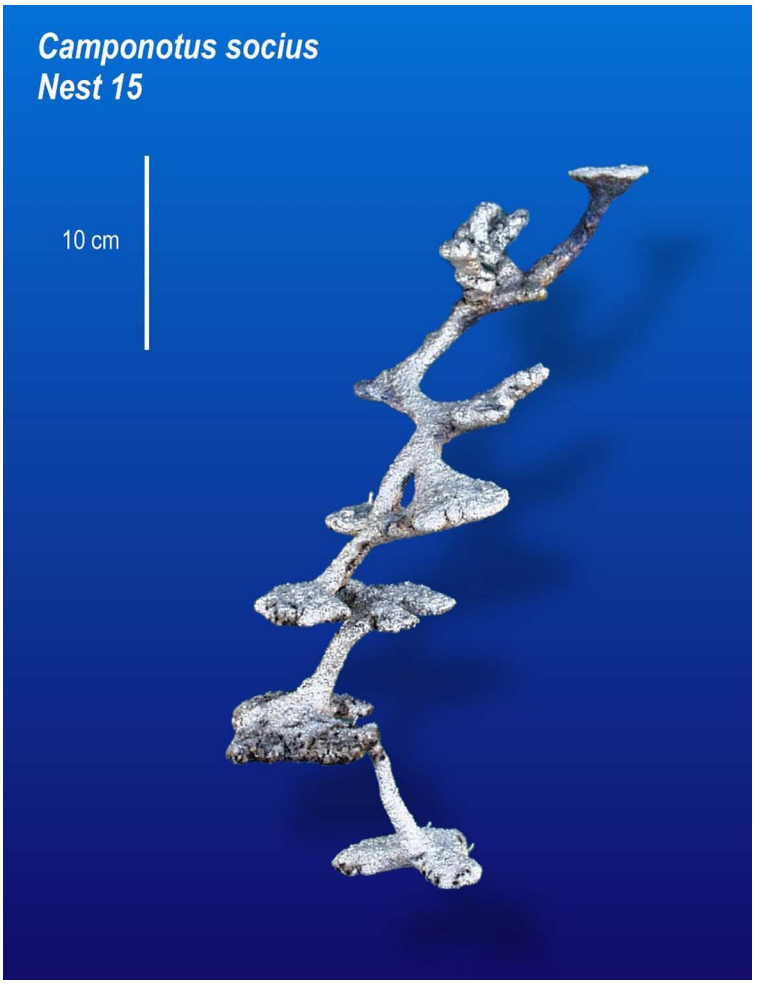
Appendix Figure 14. Non-stereo images of nest casts. Cast in Appendix 14 is of plaster, the remainder of zinc or aluminum.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



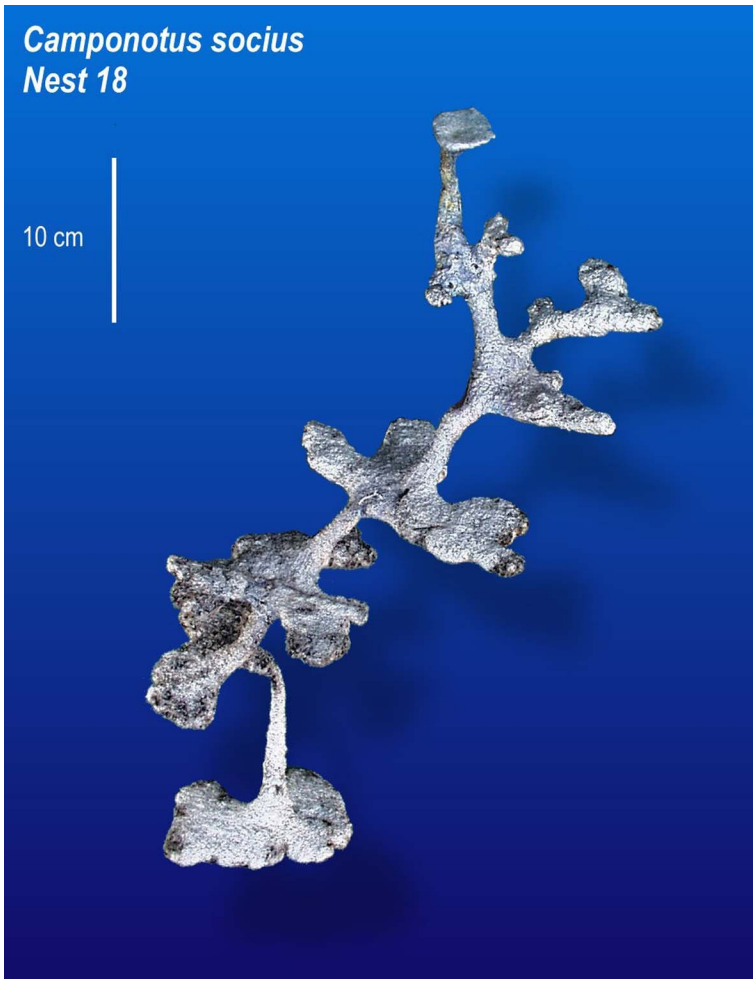
Appendix Figure 15. Non-stereo images of nest casts. Cast in Appendix 14 is of plaster, the remainder of zinc or aluminum.



Appendix Figure 16. Non-stereo images of nest casts. Cast in Appendix 14 is of plaster, the remainder of zinc or aluminum.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use

Appendix Figures



Appendix Figure 17. Non-stereo images of nest casts. Cast in Appendix 14 is of plaster, the remainder of zinc or aluminum.

Downloaded From: https://complete.bioone.org/journals/Journal-of-Insect-Science on 29 Mar 2024
Terms of Use: https://complete.bioone.org/terms-of-use