

1 **First Report of Bilateral Gynandromorphism in the Australian Ant, *Dolichoderus***
2 ***scrobiculatus* (Mayr, 1876) (Hymenoptera: Formicidae)**

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11 **Abstract**

12 Gynandromorphism is a rare developmental phenomenon producing genetically
13 chimeric individuals expressing both male and female phenotypes simultaneously. Here,
14 I describe the morphological anomalies arising from a case of bilateral worker-male
15 gynandromorphism in the Australian ant *Dolichoderus scrobiculatus* (Mayr, 1876),
16 collected during a pitfall survey of native ant fauna. The specimen exhibits a pronounced
17 bilateral mosaic distribution of morphological sex characters along the longitudinal body
18 axis: male traits are explicitly restricted to the right side, although some female
19 characters are also present there, while no male morphology is externally apparent on
20 the left. Potential implications of the condition in relation to colony-level social
21 interaction and individual behaviour are discussed. This record contributes to the limited
22 number of reports of gynandromorphism in the Formicidae and for the genus
23 *Dolichoderus*.

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26 **KEYWORDS**

27 Ergatandromorph, teratology, sex mosaic
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Introduction

Historically perceived as “veritable entomological nightmares” and “monstrosities” (Creighton, 1928; Wheeler, 1937), gynandromorphs are organisms which simultaneously display both male and female characters (Wheeler, 1937; Donisthorpe, 1929). Gynandromorphism is a rare process arising from defects during embryonic or post-embryonic development (Mariano et al., 2022). True gynandromorphs are genetically chimeric individuals exhibiting male–female phenotypes in a bilateral or patchwork mosaic, whereas intercastes and intersexes are genetically uniform individuals expressing, respectively, caste phenotypes that are intermediate between or opposite to those expected for their genetic sex, or intermediate sexual phenotypes (Heinze and Trenkle, 1997; Narita et al., 2010; Yang & Abouheif, 2011; but see Fusco and Minelli, 2023). In social Hymenoptera, gynandromorphs can involve combinations between males and the various castes of females (workers, soldiers and gynes) (Mariano et al., 2022). Gynandromorphism has now been reported for approximately 82 ant species from 37 genera in 6 subfamilies (Table 1 in Supplementary material).

Contemporary researchers may consider Formicidae exhibiting such somatic developmental abnormalities as opportunistic model systems to better understand modularity, evolvability, phenotypic variability, sex and caste determination, morphophysiology, intraspecific trait variability, nestmate recognition, and their astounding tolerance for developmental instability (Narita et al. 2010; Yang & Abouheif, 2011; Mariano et al., 2022).

Despite their relative detectability arising from the pronounced nature of sexual dimorphism in social insects (Yang and Abouheif, 2011) and phenotypical plasticity and morphological caste differentiation characters of ants (Mariano et al., 2022), gynandromorphic ants have, for the last two centuries, proven infrequently encountered and lesser-so formally described. Collections are likely depauperate of gynandromorphs due to probable high intrinsic mortality of individuals, social expulsions from nests resulting from low perceived (or actual) reproductive fitness (Mariano et al., 2022), and their generally low frequency within natural populations (Skvarla and Dowling, 2014; but see Donisthorpe, 1946; Weber, 1957; Kinomura and Yamauchi, 1994). However, Berndt and Kremer (1982) experimentally induced multiple forms of gynandromorphism in laboratory colonies of *Monomorium pharaonis* (Linnaeus, 1758) by heat-shocking larvae during development. Detailed mechanisms of gynandromorphic development within the Formicidae are described in Mariano et al. (2022), Yang and Abouheif (2011) and references therein.

Dolichoderus scrobiculatus (Mayr, 1876) is an endemic Australian species of the subgenus *Hypoclinea* Mayr, 1855 with widespread distribution along the eastern coast, known from as far north as the Cape York Peninsula and south to north-eastern New South Wales (Shattuck and Marsden, 2013), and a record from the Arnhem escarpment of Kakadu National Park in the Northern Territory (Andersen et al., 2018). Shattuck and Marsden (2013) provide note that the species can be found in savannah woodlands to

rainforests, nests in tussocks and under rocks, harvests honeydew from aphids and other Hemiptera, with low vegetation being the predominant foraging strata of workers. The ant has been implicated in ant-butterfly mutualisms, recorded tending to the larvae of *Theclines thes miskini* (Lucas, 1889), *Lampides boeticus* (Linnaeus, 1767) (Eastwood and Fraser, 1999; Eastwood et al., 2008) and a late instar larva of *Nesolycaena medicea* Braby (Braby, 2012) (all Lepidoptera: Lycaenidae).

Following contemporary terminology proposed by Mariano et al. (2022), the specimen described and photographed here is best described as a bilateral worker-male gynandromorph. For brevity, however, I adopt the terminology of Campos et al. (2011) and refer to this specimen as an ‘ergatandromorph’ (male-worker morph). Henceforth, I also employ the term ‘morphotypical’ to describe morphological characters normally present in the sterile female (worker) caste of *D. scrobiculatus* but clearly modified in the unique ergatandromorphic individual presented here. To my knowledge, this represents the first published account of ergatandromorphism in this species. Torossian (1974) reported an ergatandromorph of the Palearctic species *Dolichoderus quadripunctatus* (Linnaeus, 1771), Mariano et al. (2022) describe other teratological deformities observed in a male of the Neotropical species *Dolichoderus attelaboides* (Fabricius, 1775), and Tripathy et al. (2026) report an intercaste individual of the Palearctic species *Dolichoderus taprobanae* (Smith, F., 1858).

Materials and Methods

Taxonomic identification of specimen

Despite its pronounced morphological disparities from a morphotypical female, this specimen is still readily identifiable as *D. scrobiculatus* using Shattuck’s (1999) genus-level keys and Shattuck and Marsden’s (2013) species-level keys, provided the morphotypical (left) side is considered.

Collection and preparation of specimens

The ergatandromorphic specimen of *D. scrobiculatus* was collected in a soil-surface interface pitfall trap during a field survey at Wyaralong, Queensland, Australia (27.940°S, 152.861°E) between 26 September and 3 October 2025. The site was characterised by primary sclerophyll forest dominated by ironbark *Eucalyptus* spp. L'Hér. (Myrtaceae), weedy foliage such as Billygoat weed (*Ageratum houstonianum* Miller) (Asteraceae) and sandy soils (Bruce Tiumalu, pers. comm.). Thirteen morphotypical *D. scrobiculatus* were collected on nearby surveying sites prior to collection of the ergatandromorph, which was the only *D. scrobiculatus* represented in the trap that collected it. This pitfall also captured the ant genera *Rhytidoponera* Mayr, *Iridomyrmex* Mayr, and *Nylanderia* Emery, as well as other invertebrates of the orders Araneae, Coleoptera, Collembola, Diptera, Hemiptera, Hymenoptera, and Isopoda.

Following pitfall processing on 11 November 2025, the specimen was discovered and washed in 98% denatured ethanol (2% isopropyl alcohol) for approximately five minutes to remove external debris and propylene glycol used as the pitfall preservative. It was then point-mounted for photographing and long-term storage purposes. The comparative *D. scrobiculatus* specimen (Figs. 1b, d and f) was prepared in the same manner at a later date. Both specimens are currently held in the author's personal collection.

All images (Figs. 1-3) were captured using a Nikon SMZ25 stereomicroscope fitted with a Nikon SHR Plan Apo 1x objective lens, an integrated digital camera, and a Nikon C-FIDH dual-arm LED lighting module. Images were taken using NIS-Elements software (version 5.02.03, Build 1273) and were post-processed using the GNU Image Manipulation Program (GIMP) (version 3.0.6) to enhance the morphological detail and visual clarity. Final figure preparation and editing were carried out in Inkscape (version 1.4.3).

Results

Description of *D. scrobiculatus* ergatandromorph

The specimen exhibits a mosaic distribution of morphological sex characters along the longitudinal body axis (Fig. 1). Male traits are explicitly restricted to the right side, though some female characters are also present there, while no male morphology is externally apparent on the left side. Below, I describe the externally visible morphological abnormalities for each major body tagma.

Head: The specimen displays morphotypical female characters on the left side of the head, while the right side displays male characters (as oriented in Figs. 1e and 2). Compared with the female side, the male side shows a distinctly larger eye, a reduced and darker mandible, a lateral (on the right side) and medial ocellus typical of the male caste, male antennal morphology (although funicular segments beyond the seventh distal from the scape had been damaged and lost). Overall, the head morphology on the right side approximates that of a male.

Interestingly, the lateral ocellus on the left side did not develop, vestigial or otherwise. This is expected, as workers in this genus lack this feature, and the left side of the head is morphologically female in this specimen. This emphasises the strict bilateral nature of cephalic gynandromorphic development observed here.

The general head deformity and asymmetry of the anterolateral clypeal margin and mandible appear to have distorted the positioning of the left mandible, with the masticatory margin exceeding the typical perpendicular angle relative to the anteromedial clypeal margin at rest (see Fig. 1e-f). This may also result from the absence of a reciprocal, equivalently sized mandible on the right side, which under normal conditions could physically limit mandibular over-closure. Overall, the head appears tilted to the right (Fig. 2).

Alitrunk/mesosoma: The right-side pronotum exhibits male development, with a noticeable reduction in the size and anterolateral development of the pronotal shoulder and a shallower depth of surface fovea compared with the left (Fig. 1c-d). The foreleg on the right side also appears morphologically male and lacks the distinctive red colouration prominent on the morphotypical trochanter, distal femur, tibia and tarsal segments. On the right side of the mesonotum, a wing scar is present (Fig. 3), although it is unclear whether the wing was removed, damaged, or failed to develop entirely.

Petiole: The right side of the petiole exhibits abnormal development, lacking the distinct anterolateral expansion visible in dorsal view (compare Figs. 1c-d). It also lacks the typical posteroventral development of the sub-petiole (compare Figs. 1a-b). These right-sided differences presumably reflect the expression of male morphology in this region.

Gaster: Overall, the gaster appears predominantly female. However, the anterolateral surface of the first gastral tergite (AIII) lacks dense pubescence and erect hairs, presenting as a 'bald patch' that exposes the underlying surface sculpturing (Fig. 1a). It remains unclear whether this feature corresponds to male morphology or represents another teratological defect.

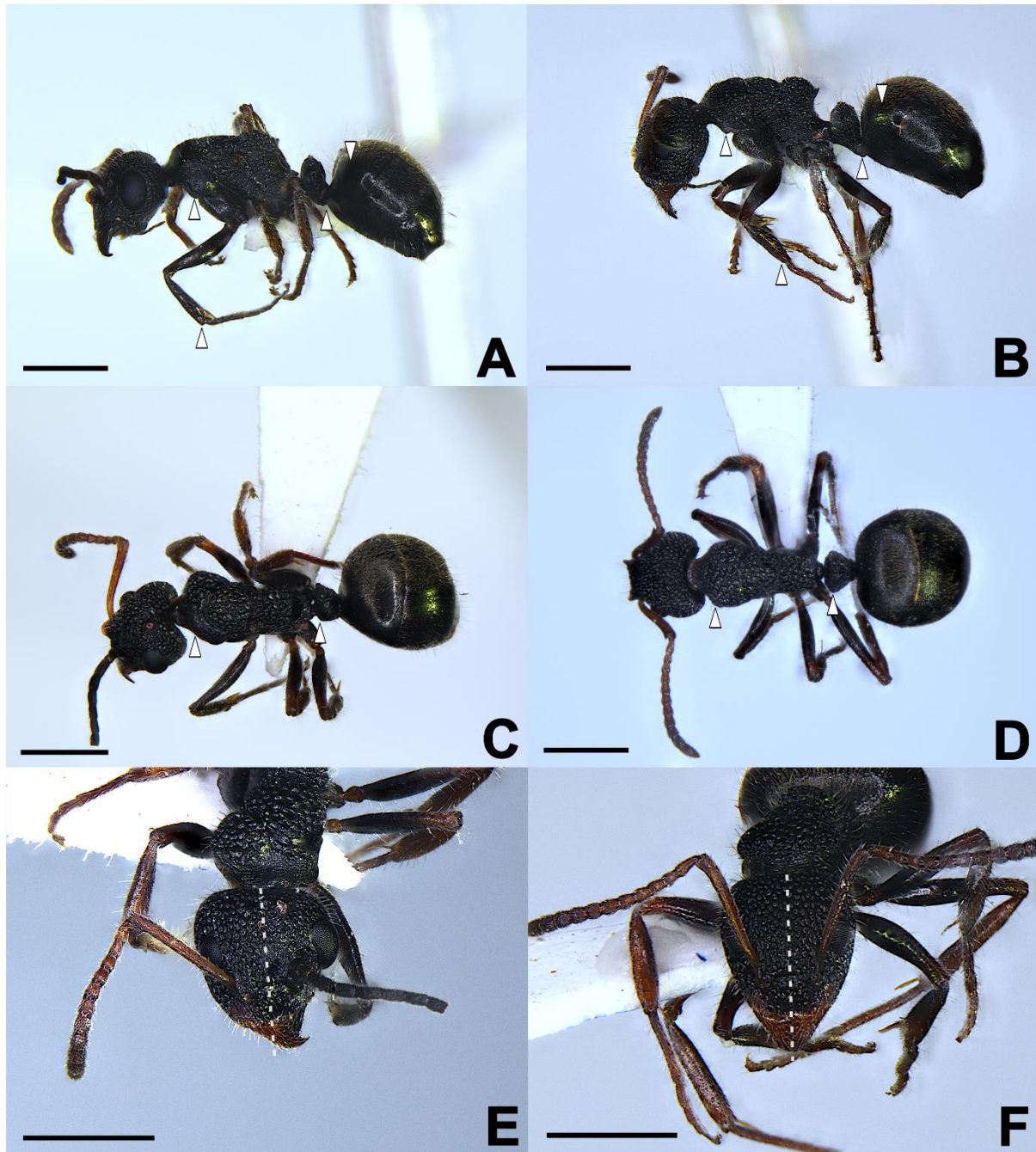


Fig 1. Ergatandromorphic *Dolichoderus scrobiculatus* (A, C, E) shown in profile, dorsal, and full-face views, respectively. Morphotypical female worker of *D. scrobiculatus* (B, D, F) shown in profile, dorsal, and full-face views, respectively. White arrows on A, B, C and D indicate regions with subtle morphological changes

174 resulting from differing sexual phenotypic expression. Lines on E and F mark the midline of the head. Scale
175 bars = 1mm.

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178 **Fig 2.** Close up of head of ergatandromorphic *Dolichoderus scrobiculatus*, oriented to show the
179 mandibular masticatory margin near-vertical, highlighting the asymmetry between the female (left) and
180 male (right) mandible and the rightward head tilt of the specimen. The prominent right-side lateral and
181 medial ocelli are indicated by white arrows. Notably, the left-side lateral ocellus is absent. Scale bar =
182 0.5mm.



Fig 3. Close-up photograph of an ergatandromorphic *Dolichoderus scrobiculatus*, with a wing scar marked with a white circle. Scale bar = 0.5mm.

Discussion

This paper documents a rare developmental anomaly in the Australian ant species *Dolichoderus scrobiculatus* through a case of bilateral male-worker gynandromorphism and characterises the resulting morphological asymmetries along the lateral body axis. Behavioural data for gynandromorphic ants remains scarce, with most documented accounts of the condition in the Formicidae focussing on aberrant morphological characters, thus leaving the potential effects of such a condition on colony function and individual behaviour largely unexplored.

The behavioural implications of bilateral male-worker gynandromorphism in this *D. scrobiculatus* specimen cannot be determined with certainty as its incidence is represented by a single deceased individual that was not observed while alive. However, because the specimen was recovered from a pitfall trap, which are used to entrap surface-active invertebrates (New, 1998), it is plausible that prior to entrapment the individual (1) was engaged in worker-typical foraging behaviour, (2) had attempted to partake in a mating event (despite lacking apparent reproductive genitalia), or (3) was expelled from its natal colony by nestmates.

Yang and Abouheif (2011) reported that a *Pheidole morrisi* Forel gynandromorph “seemed to be a functional member of its colony” and references therein observed the same phenomena in other species, lending speculative support to the first hypothesis (Wheeler, 1937; Donisthorpe, 1946; Pearson and Child, 1980; Kinomura and Yamauchi, 1994; Heinze and Trenkle, 1997; Yoshizawa et al., 2008; see also Chiyoda et al., 2023). Conversely, the latter hypothesis is also plausible, as Mariano et al. (2017; 2022) documented gynandromorphic individuals collected from the surrounds of their nests and attributed their frequent out-of-nest occurrence to colony expulsion driven by nestmate recognition of reduced reproductive fitness (but see below for an alternative explanation). It therefore remains possible that, following the event of an expulsion, the *D. scrobiculatus* ergatandromorph dispersed some distance from its nest before encountering the pitfall trap. This scenario is consistent with the absence of other *D. scrobiculatus* in the same trap, a contrast to earlier surveys on nearby sites in which this species was commonly collected in multiples (Falls, unpubl. data).

Relevant to the individual presented here, Mariano et al. (2022) raise the question of how bilateral gynandromorphs process sensory information received by their strongly dimorphic antennal structures and specific receptors. As one of the primary sensory organs of the head, antennae mediate communication, behavioural and physiological responses; in males, detection of chemical signals via the antennae underlies attraction to females (Mariano et al., 2022). Torrosian (1974) observed antennation behaviour between an ergatandromorphic *Dolichoderus quadripunctatus* and its nestmates, noting that it displayed a “significantly simplified antennal ritual” which appeared to inhibit stomodeal and proctodial trophallactic exchanges. Torrossian also states that, via its own attitude, the individual “flee[d] from his fellow creatures most of the time” (In this context, “his” was used to describe a specimen that was not uniformly genetically male). This behaviour subsequently resulted in a type of social exclusion not explicitly enforced by nestmates, potentially representing an alternative mechanism of colony-level social expulsion to that proposed by Mariano et al. (2017). Ultimately, without direct observation of the living individual described here, any behavioural inferences remain speculative.

It remains important to document these rare occurrences of gynandromorphism as they may provide a meaningfully useful model for understanding developmental, morphological, social, physiological and evolutionary processes of social insects including ants. If for no other reason, these fortuitously collected “veritable entomological nightmares” continue to fascinate and captivate myrmecologists, as they have for nearly two centuries.

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Supplementary Materials

Table 1: List of published and recorded accounts of gynandromorphic Formicidae. The first column lists species as they were reported at the time of publication, with the second column amending for contemporary taxonomic classification. The third column lists the condition of the specimen(s) as reported by their respective authors. In the Supplementary material of Mariano et al. (2022), a more comprehensive table is provided, including additional records of anomalous teratology.

Reported species	Senior synonym	Reported condition(s)	Reference(s)
<i>Acromyrmex octospinosus</i>	<i>Acromyrmex octospinosus</i> (Reich, 1793)	Gynandromorph	Wheeler (1937)
<i>Amblyopone australis</i>	<i>Amblyopone australis</i> Erichson, 1842	Gynandromorph	Haskins (1951)
<i>Anergates atratulus</i>	<i>Tetramorium atratulum</i> (Schenck, 1852)	Gynandromorph	Described by Adlerz in Donisthorpe (1929)
<i>Azteca instabilis</i>	<i>Azteca instabilis</i> (Smith, F. 1862)	Gynandromorph	Described by Forel in Wheeler (1903)
<i>Bothriomyrmex communista</i>	<i>Bothriomyrmex communista</i> Santschi, 1919	Gynandromorph	Described by Karawajew in Donisthorpe (1929)
<i>Camponotus (Colobopsis) albocinctus</i>	<i>Camponotus albocinctus</i> (Ashmead, 1905)	Dinergatandromorph	Wheeler (1919)
<i>Camponotus ligniperdus</i>	<i>Camponotus ligniperda</i> (Latrielle, 1802)	Gynandromorph	Described by Klapálek in Wheeler (1903)
<i>Camponotus yamaokai</i>	<i>Camponotus yamaokai</i> Terayama & Satoh, 1990	Ergatandromorph	Chiyoda et al. 2023
<i>Cardiocondyla batesi</i> Forel var. <i>nigra</i> Forel	<i>Cardiocondyla nigra</i> Forel, 1905	Gynandromorph	Wheeler (1914); Described by Santschi in Donisthorpe (1929)
<i>Cardiocondyla emeryi</i>	<i>Cardiocondyla emeryi</i> Forel, 1881	Gynandromorph	Heinze & Trenkle (1997)
<i>Cardiocondyla kagutsuchi</i>	<i>Cardiocondyla kagutsuchi</i> Terayama, 1999	Gynandromorph / ergatandromorph	Yoshizawa et al. 2008
<i>Cardiocondyla minutior</i>	<i>Cardiocondyla minutior</i> Forel, 1899	Gynandromorph	Wheeler (1931)
<i>Cardiocondyla wroughtoni</i> var. <i>hawaiiensis</i>	<i>Cardiocondyla wroughtonii</i> (Forel, 1890)	Gynandromorph	Wheeler (1931)
<i>Cataglyphis albicans</i>	<i>Cataglyphis albicans</i> (Roger, 1859)	Gynandromorph	Described by Santschi in Donisthorpe (1929); Wheeler (1931)
<i>Cataglyphis</i> sp.	<i>Cataglyphis</i> sp. Foerster, 1850	Gynandromorph	AntWiki.org (2026)
<i>Cephalotes atratus quadridens</i>	<i>Cephalotes atratus</i> (Linnaeus, 1758)	Gynandromorph	Wheeler (1937)
<i>Diacamma</i> sp.	<i>Diacamma</i> sp. Mayr, 1862	Gynandromorph	Dobata et al. 2011
<i>Dinoponera quadriceps</i>	<i>Dinoponera quadriceps</i> Kempf, 1971	Harlequin gynandromorph	Mariano et al. 2022
<i>Dolichoderus scrobiculatus</i>	<i>Dolichoderus scrobiculatus</i> (Mayr, 1876)	Ergatandromorph	Current study
<i>Ectatomma tuberculatum</i>	<i>Ectatomma tuberculatum</i> (Olivier, 1792)	Harlequin gynandromorph	Mariano et al. 2022
<i>Epipheidole inquilina</i>	<i>Pheidole inquilina</i> (Wheeler, W.M., 1903)	Gynandromorph	Wheeler (1903)
<i>Formica exsecta</i>	<i>Formica exsecta</i> Nylander, 1846	Gynandromorph	Described by Forel in Wheeler 1903
<i>Formica lugubris</i>	<i>Formica lugubris</i> Zetterstedt, 1838	Gynandromorph	Jan Ove et al. 2016
<i>Formica microgyna</i>	<i>Formica microgyna</i> Wheeler, W.M., 1903	Gynandromorph	Wheeler (1903)
<i>Formica nitidiventris</i>	<i>Formica pallidefulva</i> Latreille, 1802	Ergatandromorph	Creighton (1928)

<i>Formica rufa</i>	<i>Formica rufa</i> Linnaeus, 1761	Gynandromorph	Forbes (1954)
<i>Formica rufibarbis</i>	<i>Formica rufibarbis</i> Fabricius, 1793	Gynandromorph	Described by Forel in Wheeler (1903)
<i>Formica sanguinea</i>	<i>Formica sanguinea</i> Latreille, 1798	Ergatandromorph, Gynandromorph	Described by Tischbein, and Klug in Wheeler (1903)
<i>Formica truncicola</i>	<i>Formica truncorum</i> Fabricius, 1804	Gynandromorph	Described by Forel in Wheeler (1903)
<i>Gnamptogenys</i> sp. (male)	<i>Gnamptogenys</i> sp.	Harlequin gynandromorph	Mariano et al. 2022
<i>Harpagoxenus sublaevis</i>	<i>Harpagoxenus sublaevis</i> (Nylander, 1849)	Gynandromorph	Buschinger & Stoewesand (1971)
<i>Iridomyrmex constrictus</i>	† <i>Yantaromyrmex constrictus</i> (Mayr, 1868)	Gynandromorph	Wheeler (1914)
<i>Lasius (Acanthomyops) latipes</i>	<i>Lasius latipes</i> (Walsh, 1863)	Gynandromorph	Wheeler (1919)
<i>Leptothorax acervorum</i>	<i>Leptothorax acervorum</i> (Fabricius, 1793)	Gynandromorph	Buschinger & Stoewesand (1971)
<i>Leptothorax gredleri</i>	<i>Leptothorax gredleri</i> Mayr, 1855	Gynandromorph	Buschinger & Stoewesand (1971)
<i>Leptothorax kutteri</i>	<i>Leptothorax kutteri</i> Buschinger, 1966	Gynandromorph	Jan Ove et al. 2016
<i>Leptothorax muscorum</i>	<i>Leptothorax muscorum</i> (Nylander, 1846)	Gynandromorph	Buschinger & Stoewesand (1971)
<i>Leptothorax nylanderi</i>	<i>Temnothorax nylanderi</i> (Foerster, 1850)	Gynandromorph	Buschinger & Stoewesand (1971)
<i>Leptothorax obturator</i>	<i>Temnothorax obturator</i> (Wheeler, W.M., 1903)	Gynandromorph	Wheeler (1903); Donisthorpe (1929)
<i>Leptothorax tuberum</i>	<i>Temnothorax tuberum</i> (Fabricius, 1775)	Gynandromorph	Described by Adlerz in Wheeler (1903)
<i>Monomorium floricola</i>	<i>Monomorium floricola</i> (Jerdon, 1851)	Gynandromorph, ergatandromorph	Donisthorpe (1929); Campos et al. 2011
<i>Monomorium pharaonis</i>	<i>Monomorium pharaonis</i> (Linnaeus, 1758)	Gynandromorph, gynergatandromorph, ergatatandromorph, androgynergatomorph & androergatogynomorph	Berndt & Kremer (1982); Berndt & Kremer (1983); Kremer & Berndt (1986)
<i>Myrmica sabuleti</i>	<i>Myrmica sabuleti</i> Meinert, 1861	Gynandromorph	Donisthorpe (1946); Scupola (1994)
<i>Myrmica laevinodis</i> , <i>Myrmica laevinodis</i> var. <i>Ruginodo-laevinodus</i>	<i>Myrmica rubra</i> (Linnaeus, 1758)	Gynandromorph	Described by Smith, Cooke, and Wasmann in Wheeler (1903); Donisthorpe (1929)
<i>Myrmica lobicornis</i>	<i>Myrmica lobicornis</i> Nylander, 1846	Gynandromorph	Described by Meinert in Wheeler (1903)
<i>Myrmica lobulicornis</i>	<i>Myrmica lobulicornis</i> Nylander 1857	Ergatandromorph	Schifani et al. (2020)
<i>Myrmica ruginodis</i>	<i>Myrmica ruginodis</i> Nylander, 1846	Gynandromorph	Described by Forel in Wheeler 1903
<i>Myrmica rugulosa</i>	<i>Myrmica rugulosa</i> Nylander, 1849	Gynandromorph	Donisthorpe (1929); Wheeler (1931)
<i>Myrmica scabrinodis</i>	<i>Myrmica scabrinodis</i> Nylander, 1846	Ergatandromorph, Gynandromorph	Described by Wasmann in Wheeler (1903); Donisthorpe (1929)
<i>Myrmica</i> sp.	<i>Myrmica</i> sp. Latreille, 1804	Gynandromorph	Buschinger & Stoewesand (1971)
<i>Myrmica sulcinodis</i>	<i>Myrmica sulcinodis</i> Nylander, 1846	Gynandromorph	Donisthorpe (1929)
<i>Myrmecia gulosa</i>	<i>Myrmecia gulosa</i> (Fabricius, 1775)	Ergatandromorph	Crosland et al. 1988

<i>Myrmecia pavid</i>	<i>Myrmecia pavid</i> Clark, 1951	Ergatandromorph	AntWiki.org (2026)
<i>Pheidole dentata</i>	<i>Pheidole dentata</i> Mayr, 1886	Gynandromorph	Jones & Phillips (1985)
<i>Pheidole morissi</i>	<i>Pheidole morissi</i> Forel, 1886	Gynandromorph	Yang & Abouheif (2011)
<i>Pheidole pallidula</i>	<i>Pheidole pallidula</i> (Nylander, 1849)	Dinergatandromorph	Vandel (1931)
<i>Pheidole</i> sp. <i>diligens</i> group	<i>Pheidole</i> sp. <i>diligens</i> group	Gynandromorph	Mariano et al. 2022
<i>Phyracaces singaporensis</i>	<i>Lioponera singaporensis</i> (Viehmeyer, 1916)	Gynandromorph	Described by Viehmeyer in Donisthorpe (1929)
<i>Pogonomyrmex occidentalis</i>	<i>Pogonomyrmex occidentalis</i> (Cresson, 1865)	Gynandromorph	Taber & Francke (1986)
<i>Polyergus rufescens</i>	<i>Polyergus rufescens</i> (Latreille, 1798)	Gynandromorph	Described by Forel in Wheeler (1903); Jan Ove et al. 2016
<i>Polyergus rufescens</i> Latr. subsp. <i>lucidus</i> Mayr	<i>Polyergus lucidus</i> Mayr, 1870	Gynandromorph	Wheeler (1903)
<i>Polyergus samurai</i>	<i>Polyergus samurai</i> Yano, 1911	Gynandromorph	Tsuneoka (2008)
<i>Polyrhachis lamellidens</i>	<i>Polyrhachis lamellidens</i> Smith, F., 1874	Ergatandromorph	AntWiki.org (2026)
<i>Ponera coarctata pennsylvanica</i>	<i>Ponera pennsylvanica</i> Buckley, 1866	Gynandromorph	Described by Wheeler in Haskins (1951)
<i>Ponera punctatissima</i>	<i>Hypoponera punctatissima</i> (Roger, 1859)	Ergatomorph, Gynandromorph	Wheeler (1931)
<i>Promyrmecia aberrans</i>	<i>Myrmecia aberrans</i> Forel, 1900	Gynergate	Described by Tulloch in Haskins (1951)
<i>Smithistruma</i> sp.	<i>Smithistruma</i> sp. Brown, 1948	Gynandromorph	Munsee (1977)
<i>Strumigenys denticulata</i>	<i>Strumigenys denticulata</i> Mayr, 1887	Gynandromorph	Mariano et al. 2022
<i>Strumigenys filitalpa</i>	<i>Strumigenys filitalpa</i> (Brown, 1950)	Gynandromorph	Munsee (1977)
<i>Solenopsis aurea</i>	<i>Solenopsis aurea</i> Wheeler, W.M., 1906	Gynandromorph	Cokendolpher & Francke (1983)
<i>Solenopsis fugax</i>	<i>Solenopsis fugax</i> (Latreille, 1798)	Gynandromorph	Described by Santschi in Donisthorpe (1929)
<i>Solenopsis invicta</i>	<i>Solenopsis invicta</i> Buren, 1972	Gynandromorph	Hung et al. 1975
<i>Solenopsis quinquecuspis</i>	<i>Solenopsis quinquecuspis</i> Forel, 1913	Gynandromorph	Pitts (2002)
<i>Stenamma (Aphaenogaster) fulvum</i> Roger subsp. <i>aquia</i> Buckley var. <i>piceum</i> Emery	<i>Aphaenogaster picea</i> (Wheeler, W.M., 1908)	Gynandromorph	Wheeler (1903)
<i>Stenamma westwoodi</i>	<i>Stenamma westwoodii</i> Westwood, 1839	Gynandromorph	Described by Perkins in Wheeler (1903)
<i>Temnothorax turcicus</i>	<i>Temnothorax turcicus</i> (Santschi, 1934)	Ergatandromorph	Purkart et al. 2024
<i>Temnothorax curvispinosus</i>	<i>Temnothorax curvispinosus</i> Mayr, 1866	Gynandromorph	Skvarla & Dowling (2014)
<i>Tetramorium bicarinatum</i>	<i>Tetramorium bicarinatum</i> (Nylander, 1846)	Gynandromorph	Mariano et al. 2022
<i>Tetramorium guineense</i>	<i>Tetramorium guineense</i> (Bernard, 1953)	Gynandromorph	Described by Karawajew in Donisthorpe (1929)
<i>Tetramorium simillimum</i>	<i>Tetramorium simillimum</i> (Smith, F., 1851)	Gynandromorph	Described by Roger, and Meinert in Wheeler (1903); recorded by

			Santschi in Donisthorpe (1929)
<i>Vollenhovia emeryi</i>	<i>Vollenhovia emeryi</i> Wheeler, W.M., 1906	Gynandromorph	Kinomura & Yamauchi (1994)
<i>Wasmannia auropunctata</i>	<i>Wasmannia auropunctata</i> (Roger, 1863)	Gynandromorph	Mariano et al. 2022

429 † - indicates a fossil species.