

The first ergatoid male of *Platythyrea* (Hymenoptera: Formicidae: Ponerinae), with contribution to colony labor suggested by observation and comparative morphology

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Abstract

The first ergatoid male for the ant genus *Platythyrea* is discovered and described. The male of *P. sagei* FOREL, 1900, in addition to being apterous, is unique among *Platythyrea* species for bearing elongate scapes. In the field, males of *P. sagei* were observed leaving and returning to a nest with workers, some with debris in their mandibles. The male morphology of *P. sagei* is contrasted with the worker and with female / male sets for eight *Platythyrea* species. Although based on limited observation, a role in colonial labor for the ergatoid males is supported by the elongate scapes, antero-posteriorly long pronotum, and robust scapes. A lectotype of *Platythyrea sagei* is designated.

Key words: Taxonomy, lectotype designation, morphology, colony life cycle, convergent evolution, winglessness.

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Introduction

Platythyrea is the sole genus of the ponerine tribe Platythyreini, and is sister to the Ponerini (SCHMIDT 2013). The genus comprises six extinct and 38 extant species, for which males of 15 species are described (Tab. 1). *Platythyrea* species have remarkable biology, which is reviewed in SCHMIDT & SHATTUCK (2014). Particularly, there is considerable variation for reproductive females: Most species have alate queens and gamergates (reproductive workers), some species have gamergates only, one species has ergatoid queens only (apterous worker-like queens), and another has variably developed queens and gamergates which may reproduce via thelytokous parthenogenesis (MOLET & PEETERS 2006, SCHMIDT & SHATTUCK 2014). Here, we describe the ergatoid male of *P. sagei*, a species without winged queens. This is the first known ergatoid male in the genus. Contribution to colony labor by the male of *P. sagei* is suggested by observation and comparative morphology.

Materials and methods

Specimens were examined with a Wild M5 stereomicroscope with 50× maximum magnification (BEB) and a Nikon SMZ 1500 stereomicroscope with 120× maximum magnification (AAW). Measurements were carried out by AAW using a calibrated Nikon ocular micrometer. Dissections were carried out in a watch glass filled with 95% ethanol with a flattened piece of Blu-Tack (Bostik, Paris, France) for specimen stabilization. Images were montaged using stacked micrographs captured with a JVC KY-F57U

digital camera mounted on a Leica MZ 16.A microscope using Auto-Montage Pro (Synoptics Ltd., Cambridge, England); all images were edited in Photoshop CS5 (Adobe Systems Inc., California, U.S.A.) and figures were composed using Illustrator CS6 (Adobe Systems Inc., California, U.S.A.). Terminology systems are from the following sources: head (BOUDINOT & al. 2013), mesosoma (BOUDINOT 2015), and genitalia (BOUDINOT 2013). The term frontal lobe is here used to describe the structure formed by the fusion of the frontal carina itself and the dorsal torular arch, although this usage is not necessarily recommended.

Measurements and indices: All metrics were recorded in millimeters to three significant figures and are presented to two significant figures due to measurement error and / or variation in specimen orientation. Metrics are listed in alphabetical order. Two scape indices are provided to account for head capsule allometry.

- EL Eye length, maximum diameter of eye with head oblique to show full eye surface.
- GL Gaster length, maximum length of the gaster in lateral view from the anteriormost point of the first gastral segment (third abdominal) to the posteriormost point.
- HL Head length, length of head capsule from anterior clypeal margin to mid-point of posterior head margin in full-face view.
- HW Head width, maximum width of head, excluding eyes, in full-face view.

- PL Petiole length, maximum length of petiole from anterior process to posteriormost point of tergite, where it articulates with helcium.
- PnW Pronotum width, maximum width of pronotum in dorsal view.
- PW Petiole width, maximum width of petiole in dorsal view.
- SL Scape length, maximum length of scape, excluding the basal neck and condyle.
- WL Weber's length, diagonal length of mesosoma, measured in lateral view from the anterior pronotal margin, excluding the collar, to posterior extremity of propodeal lobe.
- CI Cephalic index, $HW / HL \times 100$.
- EI Eye index, $EL / HW \times 100$.
- PI Petiole index, $PW / PL \times 100$.
- SI Scape index, $SL / HW \times 100$.
- SI2 Scape index 2, $SL / WL \times 100$.

Repositories:

- AAWC Aijaz A. Wachkoo personal collection, University of Kashmir, India.
- BEBC Brendon E. Boudinot personal collection, Davis, California, U.S.A.
- JTLC John T. Longino personal collection, Salt Lake City, Utah, U.S.A.
- MHNG Muséum d'Histoire Naturelle, Geneva, Switzerland.
- PSWC Philip S. Ward personal collection, Davis, California, U.S.A.
- PUAC Punjabi University Patiala Ant Collection, Punjab, India.
- UCDC Bohart Museum of Entomology, University of California, Davis, U.S.A.

Results

Platythyrea saegei FOREL, 1900 (Figs. 1 - 14)

Platythyrea saegei FOREL, 1900: 315 (workers from India: Dharamshala and Belgaum).

Type material examined: Lectotype (worker, MHNG, CASENT0907117, present designation, "Pl. Sagei / ♀ Forel, Dharamshala (Sage) IV/5", "Typus", "Sp. Pl. Sagei / Forel.", "Coll. Forel.", "SIV/5", "ANTWEB / CASENT / 0907117").

Additional material examined: India, Himachal Pradesh: Andretta, 32.0744° N 76.5856° E, 940 m a.s.l., 11.VI.2010 (2 ♀♀, 1 ♂, PUAC), 12.VI.2010 (2 ♀♀, PUAC), 13.VI.2010 (2 ♀♀, PUAC), 11.V.2014, ground nest (12 ♀♀, 5 ♂♂, AAWC; 2 dissected ♂♂ and 2 ♀♀, UCDC), leg. Aijaz A. Wachkoo.

Diagnosis: Indomalayan species with posterodorsally bilobate petiolar node, node longer than wide in dorsal view, eye larger than 0.30 mm, and worker pedicel longer than EL and antennomere 3 length. The ergatoid male is unique among *Platythyrea* species.

Description of worker: Measurements ($n = 9$, average in parentheses): EL 0.38 - 0.40 (0.39); GL 2.58 - 2.84 (2.67); HL 1.66 - 1.71 (1.68); HW 1.32 - 1.37 (1.35); PL 0.75 - 0.78 (0.77); PnW 0.87 - 0.94 (0.90); PW 0.54 - 0.57 (0.55); SL 1.49 - 1.54 (1.51); WL 2.49 - 2.60 (2.55). Indices: CI 78.4-82.5 (80.4) (> 91 in BROWN 1975); EI 27.9 - 30.3 (28.9); PI 70.1 - 75.0 (72.4); SI 109.5 - 116.7 (112.4); SI2 58.0 - 60.2 (59.4).

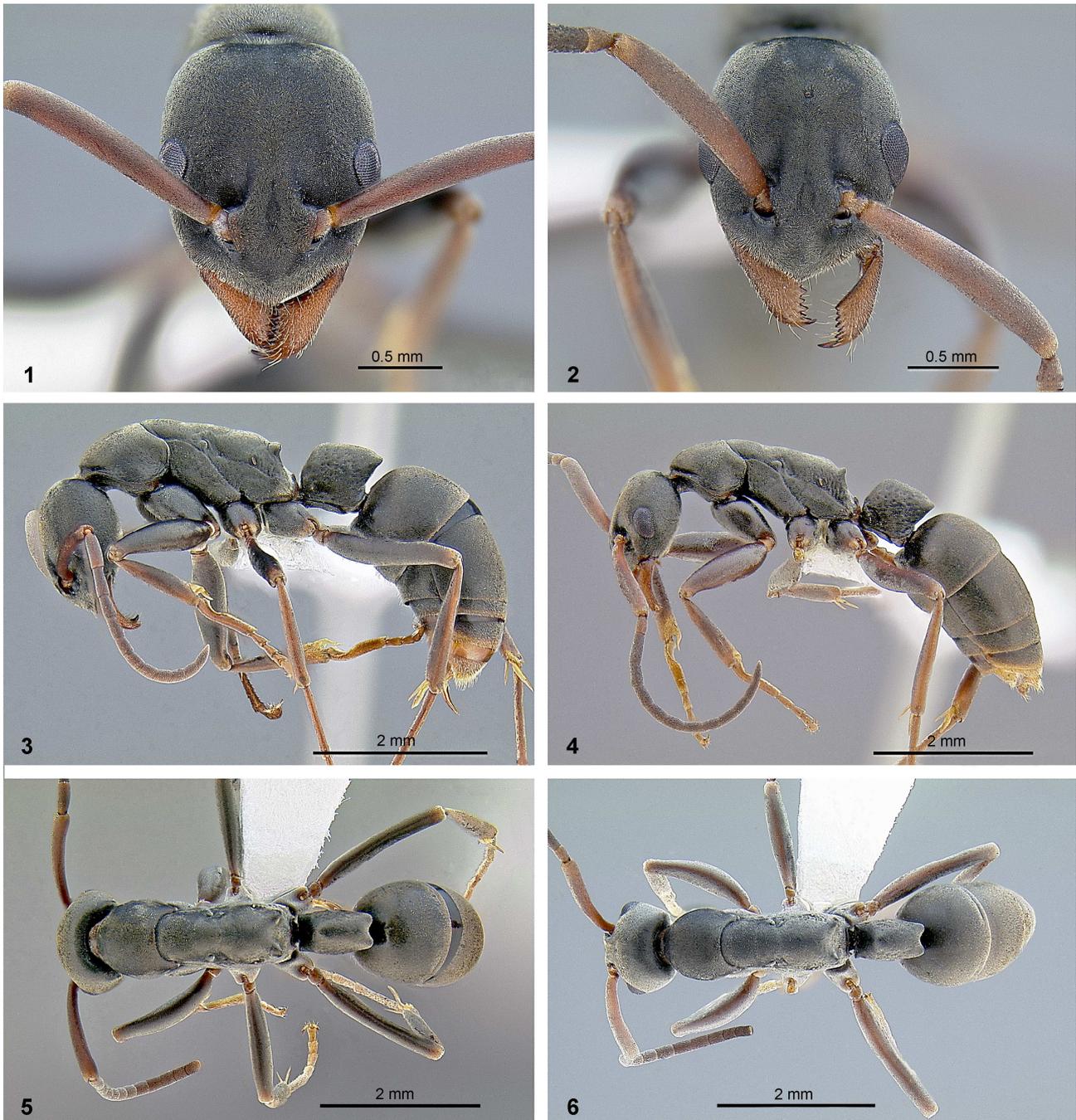
Characters not in original description: Head (Fig. 1). Frontal lobes convex, separated by a shallow, median sulcus that ends posteriorly where the lobes pass into the short, round-edged, parallel frontal carinae, visibly demarcated from clypeus. Anterior clypeal margin strongly produced, subtriangular. Posterior clypeal margin fine but reasonably distinct. Apical tooth of masticatory mandibular margin largest; other nine teeth alternating, larger and smaller. Scares long, robust, thickest beyond midlength. Compound eyes glabrous. Body after head (Figs. 3, 5). Mesosomal dorsum unevenly convex in profile; pronotum with dorsal and lateral faces meeting at a round angle; metanotum slightly constricted in middle; metanotal groove lacking; propodeal spiracle small, slit shaped. Dorsal and ventral margins of propodeal tubercles discontinuous with propodeum in profile view. Petiole subquadrate in profile, anterodorsal margin sloping anteriorly, node highest posteriorly, sides subvertical; node broadly rectangular in dorsal view, longer than wide; lateral margins feebly convex, anterior margin convex; notch between lobes of posterodorsal margin shallow, lobes narrowly separated. Cinctus between pre- and postsclerites of abdominal segment III very weak, without cross-ribbing. Coarse punctures present on body.

Description of male: Measurements ($n = 3$): EL: 0.40 - 0.41 (0.40); GL: 2.52 - 2.70 (2.63); HL: 1.44 - 1.46 (1.45); HW: 1.11 - 1.15 (1.13); PL: 0.72 - 0.80 (0.76); PnW 0.89 - 0.91 (0.90); PW: 0.50 - 0.52 (0.51); SL: 1.39 - 1.41 (1.40); WL: 2.45 - 2.50 (2.48). Indices: CI: 77.1 - 78.8 (78.1); EI 35.4 - 36.0 (35.7); PI: 65.0 - 69.4 (67.2); SI: 123.0 - 126.1 (123.9); SI2 56.4 - 56.7 (56.5).

Highly similar to worker; head (Fig. 2), body after head (Figs. 4, 6).

Exceptional characters for male of the genus (general state in brackets): Ergatoid (alate); antenna geniculate (antenna not geniculate); scape elongate, slightly shorter than head length (scape short, $SL < EL$); frontal lobes partially concealing antennal socket in full-face view (antennal sockets fully exposed); eyes only slightly larger than those of worker (eyes much larger); head capsule of similar volume as worker (volume smaller); ocelli very small, pinprick-like (ocelli well-developed); malar space elongate, slightly shorter than EL (malar space very narrow); palps reduced (palps long); legs, including coxae, robust (legs slender, weak); mesosoma of similar volume as that of worker and permanently apterous, sclerites not developed for flight (mesosoma with alate condition); pronotum, propodeum, and petiole of similar dimensions as those of worker (pronotum, propodeum, petiole smaller); helcium diameter equivalent to that of worker (helcium broader).

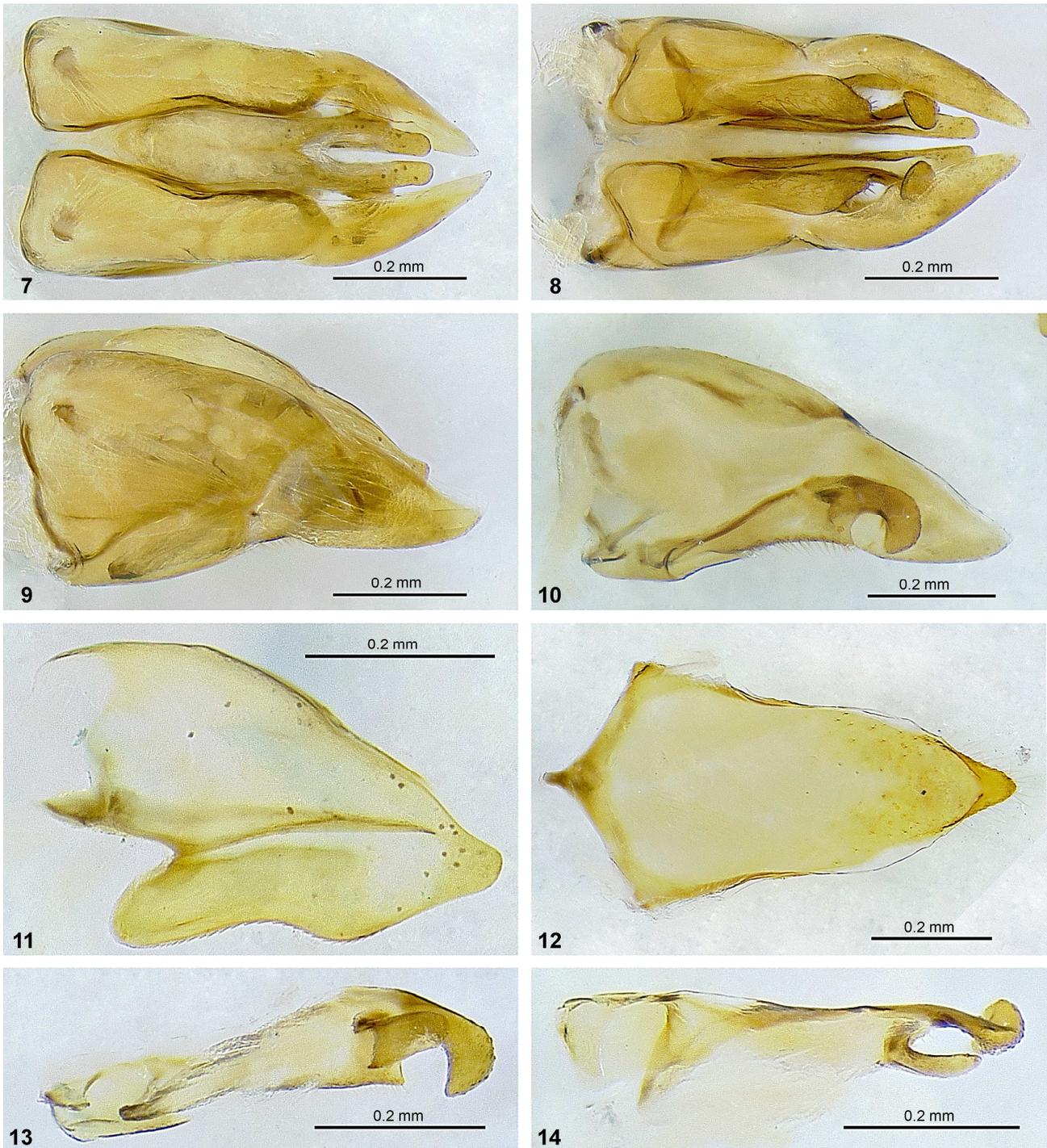
Differences from worker: Head size and proportions smaller relative to body size (differences between average metrics for each caste: $wHL - mHL = 0.23$, $wHW - mHW = 0.22$, $wCI - mCI = 2.27$, $wWL - mWL = 0.07$); antennae 13-merous; pedicel length about 0.33× that of antennomere 3; compound eyes proportionally larger (EI 35.4 - 36.0 vs. 27.9 - 30.3); ocelli present; supraclypeal area larger; distance across frons between antennal toruli narrower; masticatory margin of mandibles with 8 - 9 denticles (vs. 10); dorsal mandibular face matte (vs. shining), sculpture smaller and rougher; propodeal denticles smaller; ventral head surface (postgenal bridge), propleurae, procoxae, femora, and metasomal sterna with fewer stubble-like setae.



Figs. 1 - 6: *Platythyrea sagei* worker (1, 3, 5) and ergatoid male (2, 4, 6): (1, 2) Head, full-face view. (3, 4) Body, profile view. (5, 6) Body, dorsal view.

Genitalic description: Pygostyles present. Abdominal sternum IX (Fig. 12) large, triangular; length about $2\times$ width; spiculum short; anterolateral sternal margins tapering posterolaterally. Cupula (not figured) anteroposteriorly short; foramen genitale narrowed; dorsal face narrower than lateral faces. Basimere length about $2.33\times$ maximum width in dorsal view (Fig. 7) and about $1.3\times$ maximum height in profile view (Fig. 9); basimere dorsomedian margins parallel anteriorly for about $0.14\times$ length before diverging until past midlength before becoming parallel again for about $0.3\times$ length (Fig. 7); ventromedian margins parallel for about $0.3\times$ basimeral length before diverging (Fig. 8). Telomeres (Figs. 7 - 10) glabrous; wedge-shaped in pro-

file view, apices narrowly rounded apically; telomere maximum length about $2\times$ maximum height in profile view (Fig. 9). Basivolsella (Figs. 8, 10, 13, 14) ventrolateral margin sinuate, ventroapical angle or process acutely triangular, weakly developed; basivolsellar setae coarse, short; cuspis (Figs. 8, 13) lobate, anteroposterior length about $1.5\times$ dorsoventral height; digitus (Figs. 8, 10, 13, 14) apex clavate and twisted such that ventroapical margins almost perpendicular with digital shaft and ectal face directed posteriorly; digitus anteroposterior length about equal to dorsoventral height. Penisvalvae dorsally fused (Fig. 7); valvura (not figured) long, directed posterodorsally; valvicesps (Fig. 11) dorsal margin with two concavities and



Figs. 7 - 14: *Platythyrea sagei* male genitalia. (7) Genital capsule, dorsal view. (8) Genital capsule, ventral view. (9) Genital capsule, lateral view. (10) Right paramere and volsella, mesal view. (11) Left penisvalva, ectal view; note: valvura broken. (12) Abdominal sternum IX, mesal view. (13) Left volsella, ectal view. (14) Left volsella, dorsal view.

three convexities; apex produced, subtruncate; ventral margin strongly sinuate, with two concavities and convexities; ventral margin serrate along anterior two thirds; lateral apodeme linear, almost reaching apex. Note that genitalic proportions described above are approximate.

Comments: The non-type *Platythyrea sagei* specimens examined differ from the types by having proportionally narrower heads, but otherwise match closely. Because the worker (and male) cephalic index is smaller than 91, the specimens fail the third character in couplet 4 of BROWN'S

(1975) key to "Indo-Australian" species. *Platythyrea sagei* is one of three *Platythyrea* species known to occur in India (BHARTI 2011).

Distribution and habitat: This species seems uncommon in the Shivalik range of the Northwest Himalaya. A ground nest and individuals outside of the nest, including workers and males, were collected from dry soil in Andretta, about 30.3 km SWS from the type locality, Dharamshala, in the humid subtropical climate zone. The type locality Dharamshala and the present collection locale, An-

dretta, are hill stations (climatically temperate high elevation summer refuges) and have been described in previous publications (BHARTI & al. 2012, BHARTI & WACHKOO 2013, WACHKOO & BHARTI 2014). RAMACHANDRA & al. (2012) recorded *Platythyrea sagei* from acacia plantations, moist and dry deciduous forests, and semi evergreen forests of the Central Western Ghats south of Goa (Karnataka state) in the tropical wet climate zone. Both the Himachal Pradesh and Karnataka areas where *P. sagei* has been collected have average rainfall of at least 100 cm. The species has also been recorded from Singapore nesting in a fallen trunk (OVERBECK 1924), although this distribution record needs validation.

Biological data: Ergatoid males of *Platythyrea sagei* were encountered by AAW outside of the nest in association with workers. Workers and males were observed coming out of the nest and returning. Some males were observed to carry debris (possibly vegetative); workers of the same colony carried live minors of *Dorylus orientalis* WESTWOOD, 1835. Males were distinguishable in the field from workers by their average smaller size (average total length worker = 7.68, male = 7.31), more slender build, less agile movement, and obvious lack of a sting. In the vast majority of species male ants do not contribute to colony welfare; indeed there are no well-known exceptions. The observations recorded here suggest a limited contribution of labor by males.

Discussion

To ascertain morphological differences of *Platythyrea sagei* males from those of other *Platythyrea*, nine female / male sets of *Platythyrea* species were examined: *P. sagei* (worker, ergatoid male), *P. arnoldi* FOREL, 1913 (worker, male), *P. clypeata* FOREL, 1911 (worker, alate queen, male), *P. cribrinodis* (GERSTÄCKER, 1859) (worker / gamergate, male), *P. lamellosa* (ROGER, 1860) (worker / gamergate, male), *P. parallela* (SMITH, 1859) (worker, alate queen, male), *P. pilosula* (SMITH, 1858) (worker, male), *P. prizo* KUGLER, 1977 (worker, male), and *P. punctata* (SMITH, 1858) (worker, alate queen, male). The male of *P. sagei* differed in several characters from the males of the other eight species examined; these results are presented in the male description above.

Besides completely lacking wings and accompanying mesosomal features, the most salient difference is the elongate scapes in *Platythyrea sagei*, a unique state among known male Ponerinae. The elongated scapes of male *P. sagei* may be hypothetically explained as an adaptation for nestmate communication via antennation; alternative hypotheses should be developed and addressed in future ethological studies. The function of elongated male scapes in ants may be investigated through comparison of the dolichoderine sister lineages *Liometopum* and *Aptinoma* + *Tapinoma* (WARD & al. 2010) as males of the latter clade have convergently evolved long scapes. In general male Formicinae have elongate scapes (BOUDINOT 2015), thus observation of formicine male interaction with objects and other individuals may prove to be informative.

A character of high interest is pronotum length. KELLER & al. (2014) demonstrated that many queens have evolved elongated, worker-like pronota to handle prey during independent, non-claustral nest founding. In *Platythyrea*, male pronotum length varies considerably and, rela-

Tab. 1: Extant *Platythyrea* species for which males are described by biogeographic region; total number of species described from each region in parentheses. Oceania provided with "n / a" as the valid species was described from another region.

Region (No. spp.)	Species with male description
Nearctic (0)	n / a
Palaearctic (0)	n / a
Neotropical (9)	<i>P. prizo</i> KUGLER, 1977; <i>P. punctata</i> SMITH, 1858; <i>P. sinuata</i> (ROGER, 1860)
Afrotropical (15)	<i>P. arnoldi</i> FOREL, 1913; <i>P. conradii</i> EMERY, 1899; <i>P. cooperi</i> ARNOLD, 1915; <i>P. cribrinodis</i> (GERSTÄCKER, 1859); <i>P. lamellosa</i> (ROGER, 1860); <i>P. matoponensis</i> ARNOLD, 1915; <i>P. occidentalis</i> ANDRÉ, 1890; <i>P. schultzei</i> FOREL, 1910
Malagasy (3)	<i>P. bicuspidis</i> EMERY, 1899
Indomalaya (4)	<i>P. parallela</i> (SMITH, 1859); <i>P. sagei</i> FOREL, 1900
Australian (6)	<i>P. turneri</i> FOREL, 1895
Oceania (1)	n / a

tive to the female, may be equally long (*P. sagei*), somewhat shorter (*P. clypeata*, *P. parallela*), or much shorter (*P. cribrinodis*). This variation remains to be explained; however, males of *P. sagei* were observed to carry debris outside of the nest, suggesting that the males of this species have elongated pronota and more robust legs – relative to other male *Platythyrea* – in order to contribute to labor within the colony. A trade-off between pronotum and mesonotum size is presumed to exist, with mesonotal size correlated with development of the dorsoventral indirect flight-muscles, which are presumably not developed in *P. sagei* males. Notably, although the difference in average body size between males and workers is very small, males have absolutely and proportionally smaller head capsules than workers (see description above). After accounting for head allometry, males were found to have only slightly shorter scapes than the worker (average worker SI2 = 59.4 vs. average male SI2 = 58.4).

Two final focal characters are the mandibles and genitalia. The mandibles of *Platythyrea sagei* and alate male *Platythyrea* are very similar; if differences do occur they are subtle and may involve internal structures. Thus, at least externally, no specialization for object manipulation is suggested. It would be interesting to contrast the intra- and extranidal behavior of male *Platythyreini*, which have worker-like mandibles, and those of the Ponerini, which have as a rule highly reduced mandibles. While genitalic dimorphism has been recorded in *Technomyrmex albipes* (SMITH, 1861) which has alate and ergatoid males (OGATA & al. 1996), no significant modification of the genitalia of *P. sagei* was observed. The genitalia of *P. sagei* are well-developed and not functionally differentiated from other *Platythyrea* species.

The discovery of an ergatoid *Platythyrea* male highlights the understudied phenomenon of winglessness in male ants. How and why have ergatoid males evolved in ants? Future studies are encouraged to investigate the con-

tribution of ergatoid males to colony growth and reproduction, whether ergatoid males have evolved through colony-level selection, and how ergatoid males influence colony and population dynamics between species which are free-living and inquiline. A study of the natural history of *P. sagei* in a sociometric and sociogenetic framework is warranted (TSCHINKEL 1991, 1999, 2011).

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