



A Review of the Taxonomy, Biology and Distribution of the Social Wasps (Hymenoptera: Vespidae) of the Indian Subcontinent

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Abstract | A review of the taxonomy, biology and distribution of social wasps belonging to the subfamilies Vespinae, Polistinae and Stenogastrinae of the following 7 countries: India, Pakistan, Bangladesh, Nepal, Sri Lanka, Bhutan, and the Maldives is provided here. In India, there are at least 104 species of social wasps out of about 1100 known species worldwide and they belong to 13 genera. *Polistes* is the largest genus with 42 species followed by the genus *Ropalidia* with 27 species. Each species is provided with its current taxonomic status, along with notes on ecology, biology and distribution on the Indian subcontinent. The study of social wasps is important in several ways, as they form valuable groups to understand the evolution of social life at different levels.

Keywords: Social wasps, Taxonomy, Biology and distribution

1 Introduction

The family Vespidae consists of about 5000 species of wasps, which includes all eusocial and many solitary wasps^{23,35,64,123}. Polistinae and Vespinae are dominated by eusocial species, while Eumeninae, Euparagiinae and Masarinae contain solitary wasps. The Stenogastrine wasps are known to be facultatively eusocial.

All eusocial wasps lead a social life, consisting of colonies with a single fertile queen, few males, and many worker females. In general, the queen reproduces, and the workers give up reproduction and work for the colony. However, some leave the parental nest to found independent colonies or to join other foundresses.

Colonies of social wasps are initiated either by haplometrosis, by a single female or by pleometrosis, by a group of females^{39,93,164,165}. The Indian paper wasp *R. marginata* is known to initiate nests throughout the year and the nests are perennial^{41,133}. In this species, the nest initiation is understood to be more from May to July and relatively less from December to February¹³⁵. Studies in *R. marginata* observed that the number of foundresses can go up to 20, but most nests are initiated by less than four females^{61,62,135}.

A typical colony of social wasps contains a queen, few males, and many non-reproducing worker females, with a clearly defined hierarchy of castes, where division of labour is the main key to executing eusociality. In eusocial wasps, the queen lays eggs in cells, forages and feeds the larvae and continues doing so until the first female emerges⁹¹. On the other hand, the queen hardly takes part in extranidal activities then onwards. Instead, she engages only in nest building and egg laying. In species like *R. marginata*, though most of the worker females have the potential to reproduce, they don't reproduce in the presence of an active queen, though a few leave the parent nest to start their own colonies⁶⁰. When the queen is absent, one of the workers becomes the alpha within a few seconds and becomes a fully functional queen shortly afterwards⁶⁰. The detailed social biology and behaviour of the paper wasp, *R. marginata* is available in the book "*The Social Biology of Ropalidia marginata: toward understanding the evolution of eusociality*"⁶⁰.

As mentioned earlier different species of social wasp colonies may be initiated by a single female (Fig. 1) or by a group of females (Fig. 1). In general, most of the paper wasp species starts

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their colonies by finding a nesting site and then by making a pedicel (Fig. 1) and by adding hexagonal cells systematically as the colony grows as seen in the Indian paper wasp genera *Ropalidia* and *Vespa*. The nests may be expanded by adding more cells horizontally, or by adding more layers vertically (Fig. 1). Most of the paper wasps make open nests (Fig. 1), whereas a few builds closed nests, where combs are enclosed by paper envelopes as in the case of the genus *Vespa* and *Ropalidia montana* (Fig. 1).

Various studies about colony founding, nests' architecture, nesting habits and life cycle of Vespine wasps observed that the diversity and species richness was higher in plant substrates even though most wasps prefer to nest in man-made structures and the nesting sites of social wasps vary by species^{10,118}. Some species builds their nests on tree trunks, branches or on leaves, abandoned buildings, furniture, eaves of buildings, below stone benches, windowpanes, fences, a few in the soil and many other places as well^{2,99,105,110,115,118,143,146}. Many are placed boldly in open areas, whereas most of them make nests in fully or partially protected places (Personal observations). In a survey, one of the authors observed that the paper wasp, *R. marginata* has a strong nesting preference for closed electric boxes, the base of closed lamp posts, around transformers, etc. (Personal observation; unpublished data). An earlier study found that the genus *Polistes* usually builds single exposed combs, supported by a single pedicel in protected aerial sites, while few were concealed in tree holes or cavities¹⁰. He also observed that combs of some species of *Belonogaster* lack a petiole and were directly attached to the substratum¹⁰.

The same study observed that Stenogastrines build their nest usually in protected places, such as under cliff overhangs, in caves, rocks near waterfalls, under the vaults of small bridges or in water pipelines, i.e., dark wet places, barring few exceptions¹⁰. He also noticed that nest design among these groups of wasps were variable with species. The building materials of this group of wasps were chewed vegetable matter mixed with soil or consists mainly of mud or crumb-like pieces of rotten wood and bark, mixed with salivary secretions. He has reviewed the nesting habits of Vespidae in detail and also explained the shape and structure of the combs¹⁰.

The nesting habits and biology of many social wasps are unknown since taxonomic studies rely solely on museum specimens. Detailed natural history studies in the future will reveal the secrets of the ecology and biology of these social wasps.

The nesting biology of many social wasps in the Indian subcontinent is not understood clearly, hence information about the nesting biology of any species listed in this manuscript, when available from outside of this geographical region is incorporated here.

Though there are many taxonomic studies on Indian social Vespidae^{7,9,18,36,44,45,67,87–89,97,157,158,168}, a compilation, which discusses the ecology and biology of social Vespidae of the Indian Subcontinent is lacking and hence this study attempts to compile all the available information of social Vespidae of the Indian Subcontinent.

There are about 1100 species of social wasps across the world and among them only 104 are known to be present on the Indian Subcontinent. The biology and ecology of many social wasps of the Indian Subcontinent are less studied, barring a few exceptions,⁶⁰ compared to their taxonomy and distribution. This study attempts to add this information whenever available. An updated distribution records are also provided.

2 Materials and Methods

This study is a compilation of the information available about the social Vespidae of the Indian subcontinent. The following are the major published works examined for preparing the checklist:^{7,9,18,36–38,44,45,63–65,67–83,144,145,158,162}. We have tried to incorporate information about the ecology and biology of vespid wasps wherever they are available along with their taxonomy and distribution. The serial numbers associated with the taxonomic references are not cited in the text as it can lead to some confusion.

Images are taken by the authors (marked as '@TV' for Thresiamma Varghese and '@GK' for Girish Kumar). Nevertheless, most of the images under natural history category are taken on the Indian Institute of Science Campus by Thresiamma Varghese.

Abbreviations used for Museums/Repositories

AMSTERDAM—Zoölogisch Museum, Amsterdam, Netherlands.

BERLIN—Zoologisches Museum der Humboldt Universität, Berlin, Germany.

CAMBRIDGE—Museum of Comparative Zoology, Cambridge, USA.

GENÈVE—Muséum d'Histoire Naturelle, Genève, Switzerland.

GENOVA—Museo Civico di Storia Naturale di Genova Giacomo Doria, Genova, Italy.

KØBENHAVN—Universitetets Zoologiske Museum, København, Denmark.

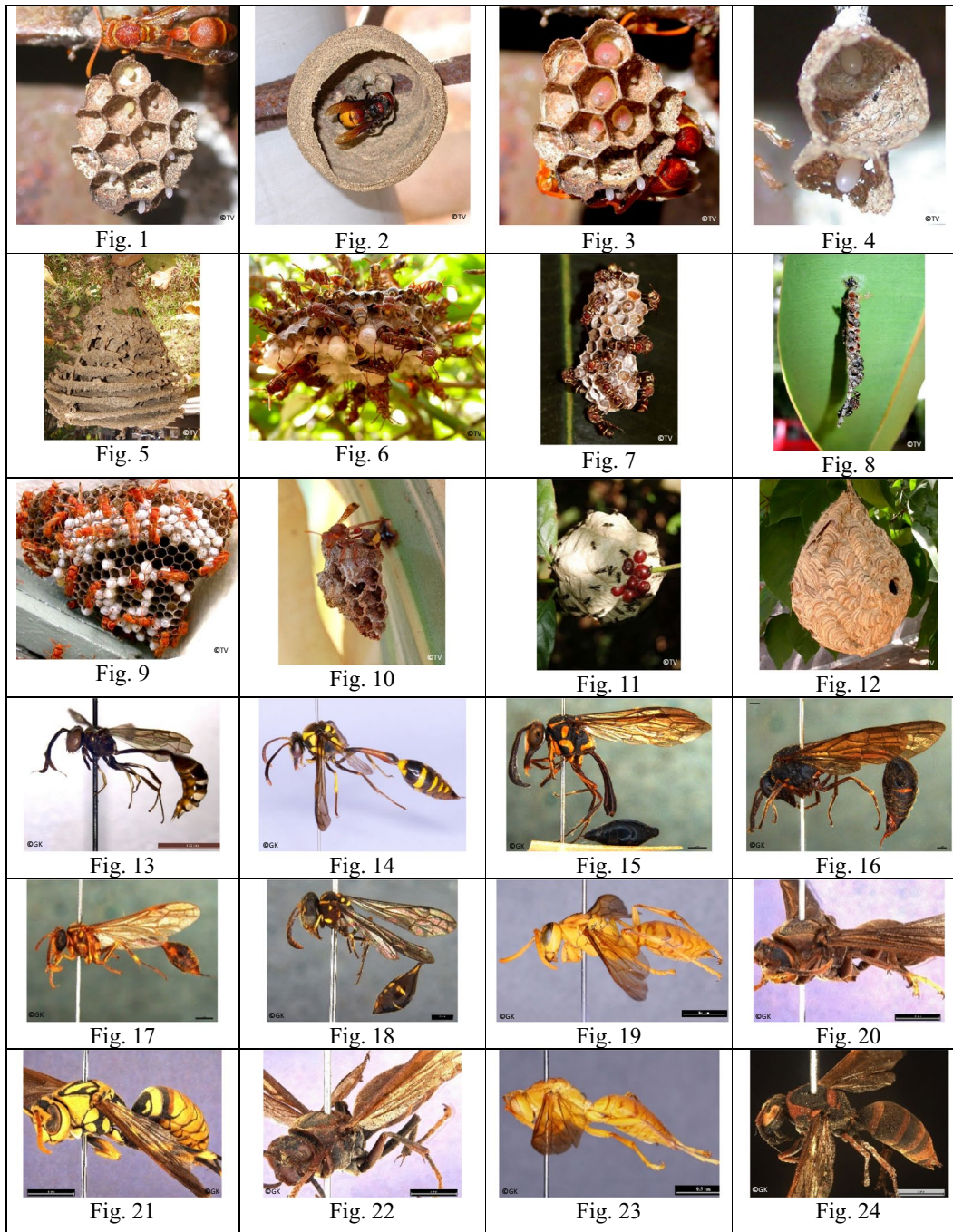


Figure 1: 1. Colony initiated by a single female, *Ropalidia marginata*. 2. Colony initiated by a single female, *Vespa tropica*. 3. Colony initiated by a group of females, *Ropalidia marginata*. 4. *Ropalidia marginata* nest showing pedicel along with two initial cells and eggs. 5. *Vespa affinis* nest opened to show different layers of combs. 6. Nest of *Polistes stigma tamulus*, on a tree branch. 7. Nest of *Ropalidia cyathiformis* on a leaf of rubber plant. 8. Nest of *Ropalidia jacobsoni*, on a leaf of rubber plant. 9. Nest of *Ropalidia marginata* on a wall. 10. Nest of *Ropalidia variegata*. 11. Nest of *Ropalidia montana* showing envelope (Location: Kalpetta, Wayanad). 12. A small nest of *Vespa affinis*. 13. *Cochlischnogaster dadugangensis*, male. 14. *Eustenogaster eximia eximioides*, male. 15. *Eustenogaster hauxwellii*, female. 16. *Eustenogaster scitula*, female. 17. *Liostenogaster nitidipennis*, female. 18. *Parischnogaster mellyi*, female. 19. *Polistes (Gyrostoma) olivaceus*, female. 20. *Polistes (Gyrostoma) rothneyi carletoni*, female. 21. *Polistes (Gyrostoma) rothneyi krombeini*, female. 22. *Polistes (Gyrostoma) rothneyi rothneyi*, female. 23. *Polistes (Gyrostoma) wattii*, female. 24. *Polistes (Polistella) adustus*, female.

KOLKATA—National Zoological Collection, Kolkata, India.

KOZHIKODE—Zoological Survey of India, Western Ghat Regional Centre, Kozhikode, India.

KRAKÓW—Instytut Systematyki i Ewolucji Zwierząt, Kraków, Poland.

LEIDEN—Nationaal Natuurhistorisch Museum (formerly Rijksmuseum van Natuurlijke Historie), Leiden, Netherlands.

LINZ—Oberösterreichisches Landesmuseum, Linz, Austria.

LONDON—British Museum (Natural History), London, England.

OXFORD—Oxford University Museum, Oxford, UK.

PARIS—Muséum national d'Histoire Naturelle, Paris, France.

PICCADILLY—Linnean Society of London, Piccadilly, London, UK.

STOCKHOLM—Naturhistoriska Riksmuseet, Stockholm, Sweden.

ST PETERSBURG—Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

STUTTGART—Staatliches Museum für Naturkunde, Stuttgart, Germany.

TORINO—Museo Regionale di Scienze Naturali di Torino, Italy.

UPPSALA—Zoological Museum, Uppsala University, Uppsala, Sweden.

VIENNA—Naturhistorisches Museum Wien, Vienna, Austria.

WASHINGTON—National Museum of Natural History, Washington, DC, USA.

YUNNAN—Kunming Institute of Zoology, Yunnan, China.

3 Results

3.1 Taxa included in this study

Family: Vespidae

Subfamily Stenogastrinae

Genus *Cochlischnogaster* Dong & Otsuka, 1997

Cochlischnogaster dadugangensis Dong & Otsuka, 1997

Genus *Eustenogaster* van der Vecht, 1969

Eustenogaster eximia (Bingham, 1890)

Eustenogaster eximia eximia (Bingham, 1890)

Eustenogaster eximia eximioides (Dover & Rao, 1922)

Eustenogaster fraterna (Bingham, 1897)

Eustenogaster hauxwellii (Bingham, 1894)

Eustenogaster scitula (Bingham, 1897)

Genus *Liostenogaster* van der Vecht, 1969

Liostenogaster nitidipennis (de Saussure, 1853)

Genus *Parischnogaster* Schulthess, 1914

Parischnogaster mellyi (de Saussure, 1852)

Subfamily Polistinae

Tribe Polistini Lepeletier, 1836

Genus *Polistes* Latreille, 1802

Polistes (Gyrostoma) gigas Kirby, 1826

Polistes (Gyrostoma) jokahamae Radoszkowski, 1887

Polistes (Gyrostoma) olivaceus (De Geer, 1773)

Polistes (Gyrostoma) rothneyi Cameron, 1900

Polistes (Gyrostoma) rothneyi carletoni van der Vecht, 1968

Polistes (Gyrostoma) rothneyi krombeini van der Vecht, 1968

Polistes (Gyrostoma) rothneyi rothneyi Cameron, 1900

Polistes (Gyrostoma) rothneyi vechti Das & Gupta, 1989

Polistes (Gyrostoma) tenebricosus Lepeletier, 1836

Polistes (Gyrostoma) wattii Cameron, 1900

Polistes (Polistella) adustus Bingham, 1897

Polistes (Polistella) angusticlypeus Gusenleitner, 2006

Polistes (Polistella) assamensis Bingham, 1897

Polistes (Polistella) dawnae Dover & Rao, 1922

Polistes (Polistella) delhiensis Das & Gupta, 1989

Polistes (Polistella) ephippium Cameron, 1900

Polistes (Polistella) khasianus Cameron, 1900

Polistes (Polistella) latinis Das & Gupta, 1989

Polistes (Polistella) lepcha Cameron, 1900

Polistes (Polistella) nigratarsis Cameron, 1900

Polistes (Polistella) opacus Gusenleitner, 2006

Polistes (Polistella) quadricingulatus Gusenleitner, 2006

Polistes (Polistella) rubellus Gusenleitner, 2006

Polistes (Polistella) sagittarius de Saussure, 1854

Polistes (Polistella) santoshae Das & Gupta, 1989

Polistes (Polistella) similis Das & Gupta, 1989

Polistes (Polistella) stigma (Fabricius, 1793)

Polistes (Polistella) stigma galathea Petersen, 1987

Polistes (Polistella) stigma novarae de Saussure, 1867

Polistes (Polistella) stigma sauensis Petersen, 1987

Polistes (Polistella) stigma tamulus (Fabricius, 1798)

Polistes (Polistella) strigosus Bequaert, 1940

Polistes (Polistella) strigosus atratus Das & Gupta, 1989

Polistes (Polistella) strigosus strigosus Bequaert, 1940

- Polistes (Polistes) associus* Kohl, 1898
Polistes (Polistes) biglumis (Linnaeus, 1758)
Polistes (Polistes) dominula (Christ, 1791)
Polistes (Polistes) gallicus (Linnaeus, 1767)
Polistes (Polistes) indicus Stolfa, 1934
Polistes (Polistes) nimpha (Christ, 1791)
 Tribe Ropalidiini Bequaert, 1918
 Genus *Belonogaster* de Saussure, 1853
Belonogaster indica (de Saussure, 1853)
Belonogaster juncea juncea (Fabricius, 1781)
 Genus *Parapolybia* de Saussure, 1853
Parapolybia escalerae (Meade-Waldo, 1911)
Parapolybia fulvinerva (Cameron, 1900)
Parapolybia indica (de Saussure, 1854)
Parapolybia nodosa van der Vecht, 1966
Parapolybia tinctipennis (Cameron, 1900)
Parapolybia varia (Fabricius, 1787)
 Genus *Polybioides* du Buysson, 1913
Polybioides gracilis van der Vecht, 1966
 Genus *Ropalidia* Guérin-Méneville, 1831
Ropalidia andamanensis Das & Gupta, 1989
Ropalidia bicolorata van der Vecht, 1962
Ropalidia birmanica Das & Gupta, 1989
Ropalidia brevita Das & Gupta, 1989
Ropalidia colorata van der Vecht, 1941
Ropalidia cyathiformis (Fabricius, 1804)
Ropalidia fasciata (Fabricius, 1804)
Ropalidia hongkongensis (de Saussure, 1854)
Ropalidia jacobsoni (du Buysson, 1908)
Ropalidia kasaragodensis Lambert & Narendran, 2005
Ropalidia marginata (Lepeletier, 1836)
Ropalidia mathematica (Smith, 1860)
Ropalidia montana Carl, 1934
Ropalidia narendrani Shareef, Kishore & Girish Kumar, 2015
Ropalidia nigrita Das & Gupta, 1989
Ropalidia ornateiceps (Cameron, 1900)
Ropalidia rufocollaris (Cameron, 1900)
Ropalidia rufoplagiata (Cameron, 1900)
Ropalidia sahyadrica Kishore, Shareef & Girish Kumar, 2014
Ropalidia santhoshae Das & Gupta, 1989
Ropalidia scitula (Bingham, 1897)
Ropalidia sculpturata Gusenleitner, 2001
Ropalidia spatulata van der Vecht, 1962
Ropalidia stigma (Smith, 1858)
Ropalidia sumatrae (Weber, 1801)
Ropalidia tamila Gusenleitner, 2004
Ropalidia variegata (Smith, 1852)
 Subfamily Vespinae
 Genus *Dolichovespula* Rohwer, 1916
Dolichovespula flora Archer, 1987
Dolichovespula intermedia (Birula, 1930)

- Dolichovespula lama* (du Buysson, 1903)
Dolichovespula sylvestris (Scopoli, 1763)
Dolichovespula xanthicincta Archer, 1981
 Genus *Provespa* Ashmead, 1903
Provespa barthelemyi (du Buysson, 1905)
 Genus *Vespa* Linnaeus, 1758
Vespa affinis (Linnaeus, 1764)
Vespa analis Fabricius, 1775
Vespa basalis Smith, 1852
Vespa bicolor Fabricius, 1787
Vespa binghami du Buysson, 1905
Vespa ducalis Smith, 1852.
Vespa dybowskii André, 1884
Vespa fumida van der Vecht, 1905
Vespa mandarinia Smith, 1852
Vespa mocsaryana du Buysson, 1905
Vespa orientalis Linnaeus, 1771
Vespa soror du Buysson, 1905
Vespa tropica (Linnaeus, 1758)
Vespa velutina Lepeletier, 1836
Vespa vivax Smith, 1870
 Genus *Vespula* Thomson, 1896
Vespula austriaca (Panzer, 1799)
Vespula flaviceps (Smith, 1870)
Vespula germanica (Fabricius, 1793)
Vespula kingdonwardi Archer, 1981
Vespula koreensis (Radoszkowski, 1887)
Vespula nursei Archer, 1981
Vespula orbata (du Buysson, 1902)
Vespula rufa (Linnaeus, 1758)
Vespula structor (Smith, 1870)
Vespula vulgaris (Linnaeus, 1758)

SYSTEMATIC ACCOUNT

Family VESPIDAE

Subfamily Stenogastrinae

Genus *Cochlischnogaster* *Cochlischnogaster* Dong & Otsuka, 1997

Cochlischnogaster Dong and Otsuka, 1997: 205, 206 (key), 210. Type species: *Cochlischnogaster dadugangensis* Dong and Otsuka, 1997.

Chalogaster Carpenter & Starr, 2000: 1, 3. Type species: *Chalogaster spatulata* Carpenter & Starr, 2000.

1) *Cochlischnogaster dadugangensis* Dong & Otsuka, 1997 (Fig. 1)

Cochlischnogaster dadugangensis Dong and Otsuka, 1994: 451.

Cochlischnogaster dadugangensis Dong & Otsuka, 1997: 207. Holotype female, Dadugang, Yunnan, China (YUNNAN).

Distribution: India: Arunachal Pradesh. *Elsewhere:* China; Vietnam⁶⁴.

Genus *Eustenogaster* van der Vecht, 1969

Eustenogaster van der Vecht, 1969: 165. Type species: *Ischnogaster micans* de Saussure, 1852.

Paravespa Bell, 1936: 1, 803, 806. Type species: *Paravespa eva* Bell, 1936.

2) *Eustenogaster eximia* (Bingham, 1890)**a) *Eustenogaster eximia eximia* (Bingham, 1890)**

Ischnogaster eximius Bingham, 1890: 244. Male "Ceylon" (LONDON).

Eustenogaster eximia; Iwata, 1976: 275 (Ethology).

Distribution: Sri Lanka. *Elsewhere*: Malaysia; Thailand³⁷.

Nesting habits: This species is known to construct pear-shaped nests from masticated bits of rotten vegetative matter in sheltered spots in the rain forest, usually beneath earth or rock overhangs along streams⁹⁹.

b) *Eustenogaster eximia eximioides* (Dover & Rao, 1922) (Fig. 1)

Stenogaster eximioides Dover and Rao, 1922: 242. Lectotype male, Nilgiri Hills, Tamil Nadu, India (KOLKATA).

Eustenogaster eximia eximioides; Das and Gupta, 1984: 402.

Distribution: India: Goa, Karnataka, Kerala, Tamil Nadu⁶⁴.

3) *Eustenogaster fraterna* (Bingham, 1897)

Ischnogaster fraterna Bingham, 1897: 377 (key), 378. Female, male, "Tenasserim" (LONDON).

Eustenogaster fraterna; Iwata, 1976: 275.

Distribution: India: Assam, Sikkim; Myanmar. *Elsewhere*: Malaysia; Thailand⁶⁴.

Nesting habits: This stenogastrine wasp *E. fraterna* builds inverted-flask shaped nests with tiny pieces of plant material which are suspended on fine rootlets or plant fibres jutting out from road-sides or stream sides^{116,117,127}.

4) *Eustenogaster hauxwellii* (Bingham, 1894) (Fig. 1)

Ischnogaster hauxwellii Bingham, 1894: 386. Female, male, "Tenasserim" (LONDON).

Eustenogaster hauxwellii; Iwata, 1976: 274.

Distribution: India: Sikkim; Myanmar. *Elsewhere*: Cambodia; Indonesia; Malaysia; Philippines; Singapore; Thailand; Vietnam⁶⁴.

5) *Eustenogaster scitula* (Bingham, 1897) (Fig. 1)

Ischnogaster scitula Bingham, 1897: 377 (key), 379. Female, "Rangit Valley, Sikkim; Margherita, Assam" (LONDON).

Eustenogaster scitula; Das and Gupta, 1984: 402.

Distribution: India: Arunachal Pradesh, Assam, Meghalaya, Sikkim; Bhutan; Myanmar. *Elsewhere*: China; Laos; Malaysia; Thailand; Vietnam⁶⁴.

Genus *Liostenogaster* van der Vecht, 1969

Liostenogaster van der Vecht, 1969, in Yoshikawa *et al.*, 165, genus. Type species: *Ischnogaster nitidipennis* de Saussure, 1853, by original designation.

6) *Liostenogaster nitidipennis* (de Saussure, 1853) (Fig. 1)

Ischnogaster nitidipennis de Saussure, 1853: 10. Male, "Selon l'étiquette, Cayenne!?? mais il est évident à mes yeux que cet insecte ne peut venir que de Java, de la Nouvelle-Guinée, ou de la Polynésie (PARIS).

Liostenogaster nitidipennis; Iwata, 1976: 275 (Ethology).

Distribution: Myanmar. *Elsewhere*: Indonesia; Malaysia; Philippines; Singapore; Thailand⁶⁴.

Genus *Parischnogaster* Schulthess, 1914

Parischnogaster Schulthess, 1914: 255. Type species: *Ischnogaster mellyi* de Saussure, 1852.

Holischnogaster van der Vecht, 1977: 60, 70. Type species: *Holischnogaster gracilipes* van der Vecht, 1977.

7) *Parischnogaster mellyi* (de Saussure, 1852) (Fig. 1)

Ischnogaster mellyi de Saussure, 1852: 25. Male, "Java" (GENÈVE).

Parischnogaster mellyi; Schulthess, 1927: 82.

Distribution: India: Andaman & Nicobar Islands, Andhra Pradesh, Arunachal Pradesh, Assam, Chhattisgarh, Meghalaya, Mizoram, Sikkim; Bhutan; Myanmar. *Elsewhere*: China; Indonesia; Malaysia; Philippines; Singapore; Thailand; Vietnam⁶⁴.

Nesting habits: The nesting biology of this species and other Stenogastrine wasps were carried out in detail and observed that its nests are with distinct combs, located on the strands of dead vegetation or on loose strands of thatch under the roofs of houses^{90,150}.

Subfamily Polistinae**Tribe Polistini Lepelletier, 1836**

Genus *Polistes* Latreille, 1802

Polistes Latreille, 1802: 363. Type species: *Vespa gallica* Linnaeus, 1767.

8) *Polistes (Gyrostoma) gigas* Kirby, 1826

Cyclostoma gigas Kirby, 1826: 36. Male, China (OXFORD).

Polistes gyrostoma de Saussure, 1854: 104, India, China.

Distribution: India: Sikkim. *Elsewhere*: China (including Hong Kong and Taiwan); Vietnam⁶⁴.

Nesting habits: An elaborate study was carried out to understand the nesting habits and nest architecture of this species¹¹⁴.

9) *Polistes (Gyrostoma) jokahamae* Radoszkowski, 1887

Polistes jokahamae Radoszkowski, 1887: 435. Female Lectotype, "Jokahama", Honshu, Japan (KRAKÓW).

Distribution: India: *Elsewhere*: China; Japan; Korea; Malaysia; Mongolia; Society Islands: Bora; Tahiti; Tuamotu Archipelago; introduced into Hawaii; Vietnam⁶⁴.

10) *Polistes (Gyrostoma) olivaceus* (De Geer, 1773) (Fig. 1)

Vespa olivacea De Geer, 1773: 582. America.

Vespa hebraea Fabricius, 1787: 292. Female, India (KØBENHAVN).

Distribution: India: Andhra Pradesh, Arunachal Pradesh, Assam, Chhattisgarh, Gujarat, Himachal Pradesh, Jammu & Kashmir, Jharkhand, Karnataka, Madhya Pradesh, Manipur, Meghalaya, Nagaland, Odisha, Rajasthan, Sikkim, Telangana, Tripura, Uttarakhand, Uttar Pradesh, West Bengal; Bangladesh; Bhutan; Myanmar; Nepal; Pakistan; Sri Lanka. *Elsewhere*: Afghanistan; Amirantes; Australia (introduced); Cambodia; Chagos Archipelago; Chile, Easter Is. (introduced); China (including Hong Kong and Taiwan); Egypt; Fiji; French Polynesia; Hawaii; Indonesia; Iran; Japan; Laos; Madagascar; Malaysia; Marianas; Mauritius; New Caledonia; New Zealand (introduced); Oman; Philippines; Réunion; Samoa; Seychelles; Singapore; Society Is.; Tanzania; Thailand; Tonga; U.S.A. (introduced); Vietnam⁶⁴.

Nesting habits: This species is known to make un-protected, one-sided symmetrical and compact (disk-like) paper comb construction with eccentric pedicel¹². A curious case of snout moth parasitising the nest of *P. olivaceus* is reported from Vietnam¹²². This species was found nesting on tree branches and walls of buildings in South India (Personal observation).

11) *Polistes (Gyrostoma) rothneyi* Cameron, 1900

a) *Polistes (Gyrostoma) rothneyi carletoni* van der Vecht, 1968 (Fig. 1)

Polistes (Megapolistes) rothneyi carletoni van der Vecht, 1968: 99, 100. Female, Kullu, Himachal Pradesh, India (WASHINGTON).

Distribution: India: Arunachal Pradesh, Assam, Jammu & Kashmir, Himachal Pradesh, Uttarakhand, Uttar Pradesh; Nepal; Pakistan⁶⁴.

b) *Polistes (Gyrostoma) rothneyi krombeini* van der Vecht, 1968 (Fig. 1)

Polistes (Megapolistes) rothneyi krombeini van der Vecht, 1968: 100. Female, Coimbatore, Tamil Nadu, India (CAMBRIDGE).

Distribution: India: Chhattisgarh, Karnataka, Kerala, Meghalaya, Tamil Nadu, Uttarakhand⁶⁴.

c) *Polistes (Gyrostoma) rothneyi rothneyi* Cameron, 1900 (Fig. 1)

Polistes rothneyi Cameron, 1900: 410. Male, Barrackpore, West Bengal, India (OXFORD).

Distribution: India: Delhi, Meghalaya, Uttarakhand, Sikkim, West Bengal; Nepal⁶⁴.

d) *Polistes (Gyrostoma) rothneyi vechti* Das and Gupta, 1989

Polistes rothneyi vechti Das and Gupta, 1984: 410. Holotype female, Manipur, India (KOLKATA).

Distribution: India: Manipur; Myanmar⁶⁴.

12) *Polistes (Gyrostoma) tenebricosus* Lepeletier, 1836

Polistes tenebricosus Lepeletier, 1836: 529. Java, Indonesia.

Distribution: India: Arunachal Pradesh, Assam, Jammu & Kashmir, Meghalaya, Mizoram, Nagaland, Sikkim, Tripura, Uttarakhand, West Bengal; Bhutan; Nepal. *Elsewhere*: China (including Taiwan); Indonesia; Philippines; Vietnam⁶⁴.

13) *Polistes (Gyrostoma) wattii* Cameron, 1900 (Fig. 1)

Polistes wattii Cameron, 1900: 416. Female, Bengal, India (LONDON).

Distribution: India: Bihar, Chhattisgarh, Delhi, Gujarat, Haryana, Himachal Pradesh, Jammu & Kashmir, Jharkhand, Madhya Pradesh, Meghalaya, Odisha, Punjab, Rajasthan, Uttarakhand, Uttar Pradesh, West Bengal; Pakistan. *Elsewhere*: Afghanistan; China; Iran; Iraq; Mauritius; Oman; Saudi Arabia; Tajikistan; Turkmenistan; U.A.E.⁶⁴.

Nesting habits: Recently, the natural history, unique nesting cycle and striking nest architecture of this species in North India is studied¹³⁴. They observed that *P. wattii* hibernates in winter as well as forms nest-free aggregations in the dry summer season. They observed that this species has a nesting cycle with two inactive periods, which no other *Polistes* is known to follow so far to maximise their survival and fitness.

14) *Polistes (Polistella) adustus* Bingham, 1897 (Fig. 1)

Polistes adustus Bingham, 1897: 397. Holotype female, Sikkim, India (LONDON).

Distribution: India: Arunachal Pradesh, Delhi, Himachal Pradesh, Jammu & Kashmir, Meghalaya, Sikkim, Uttarakhand, West Bengal; Bhutan; Nepal. *Elsewhere:* China^{64,66}.

15) *Polistes (Polistella) angusticlypeus* Guse-nleitner, 2006

Polistes (Polistella) angusticlypeus Guse-nleitner, 2006: 680. Holotype male, Shillong, Meghalaya, India (LINZ).

Distribution: India: Meghalaya⁶⁴.

16) *Polistes (Polistella) angusticlypeus* Bingham, 1897 (Fig. 2)

Polistes assamensis Bingham, 1897: 397. Female, Margherita, Assam, India (LONDON).

Distribution: India: Assam, Sikkim⁶⁴.

17) *Polistes (Polistella) dawnae* Dover & Rao, 1922 (Fig. 2)

Polistes dawnae Dover & Rao, 1922: 248. Type data: Female, Dawna Hills, Myanmar (KOLKATA).

Distribution: India: Arunachal Pradesh, Nagaland; Myanmar. *Elsewhere:* Laos; Vietnam⁶⁴.

18) *Polistes (Polistella) delhiensis* Das & Gupta, 1989 (Fig. 2)

Polistes (Stenopolistes) delhiensis Das & Gupta, 1984: 410, nomen nudum.

Polistes (Stenopolistes) delhiensis Das & Gupta, 1989: 63. Holotype female, Delhi, India (KOLKATA).

Distribution: India: Delhi. *Elsewhere:* Vietnam⁶⁴.

Nesting habits: The nests of this species are attached to broad leaves, with paper-like combs made with fine plant fibers mixed with adult oral secretion¹¹⁵.

19) *Polistes (Polistella) ephippium* Cameron, 1900

Polistes ephippium Cameron, 1900: 415. Female, Khasi Hills, Meghalaya, India (LONDON).

Distribution: India: Meghalaya⁶⁴.

20) *Polistes (Polistella) khasianus* Cameron, 1900 (Fig. 2)

Polistes khasianus Cameron, 1900: 413. Holotype female, Khasia Hills, Meghalaya, India (OXFORD).

Distribution: India: Haryana, Meghalaya, Sikkim, West Bengal. *Elsewhere:* Vietnam⁶⁴.

Nesting habits: The nest of this species is described for the first time and found that the paper-like nests of this species are attached to long leaves¹¹³.

21) *Polistes (Polistella) latinis* Das & Gupta, 1989 (Fig. 2)

Polistes (Polistella) latinis Das & Gupta, 1989: 79. Holotype female, South Andamans, India (KOLKATA).

Distribution: India: Andaman & Nicobar Islands⁶⁴.

22) *Polistes (Polistella) lepcha* Cameron, 1900 (Fig. 2)

Polistes khasianus Cameron, 1900: 415. Female, Khasi Hills, Meghalaya, India (LONDON & OXFORD).

Distribution: India: Haryana, Manipur, Meghalaya. *Elsewhere:* Laos; Vietnam⁶⁴.

23) *Polistes (Polistella) nigratarsis* Cameron, 1900 (Fig. 2)

Polistes nigratarsis Cameron, 1900: 413. Male, Barrackpore, West Bengal, India (OXFORD).

Distribution: India: Arunachal Pradesh, Goa, Karnataka, Kerala, Meghalaya, Tamil Nadu, West Bengal; Bhutan. *Elsewhere:* Vietnam⁶⁴.

24) *Polistes (Polistella) opacus* Guseleitner, 2006

Polistes (Polistella) opacus Guseleitner, 2006: 681. Holotype female, Pakyong, Sikkim, India (LINZ).

Distribution: India: Sikkim, West Bengal. *Elsewhere:* Laos⁶⁴.

25) *Polistes (Polistella) quadricingulatus* Guseleitner, 2006 (Fig. 2)

Polistes (Polistella) quadricingulatus Guseleitner, 2006: 683. Holotype female, Bhimtal, Uttarakhand, India (LINZ).

Distribution: India: Jammu & Kashmir, Uttarakhand; Nepal; Pakistan. *Elsewhere:* Laos⁶⁴.

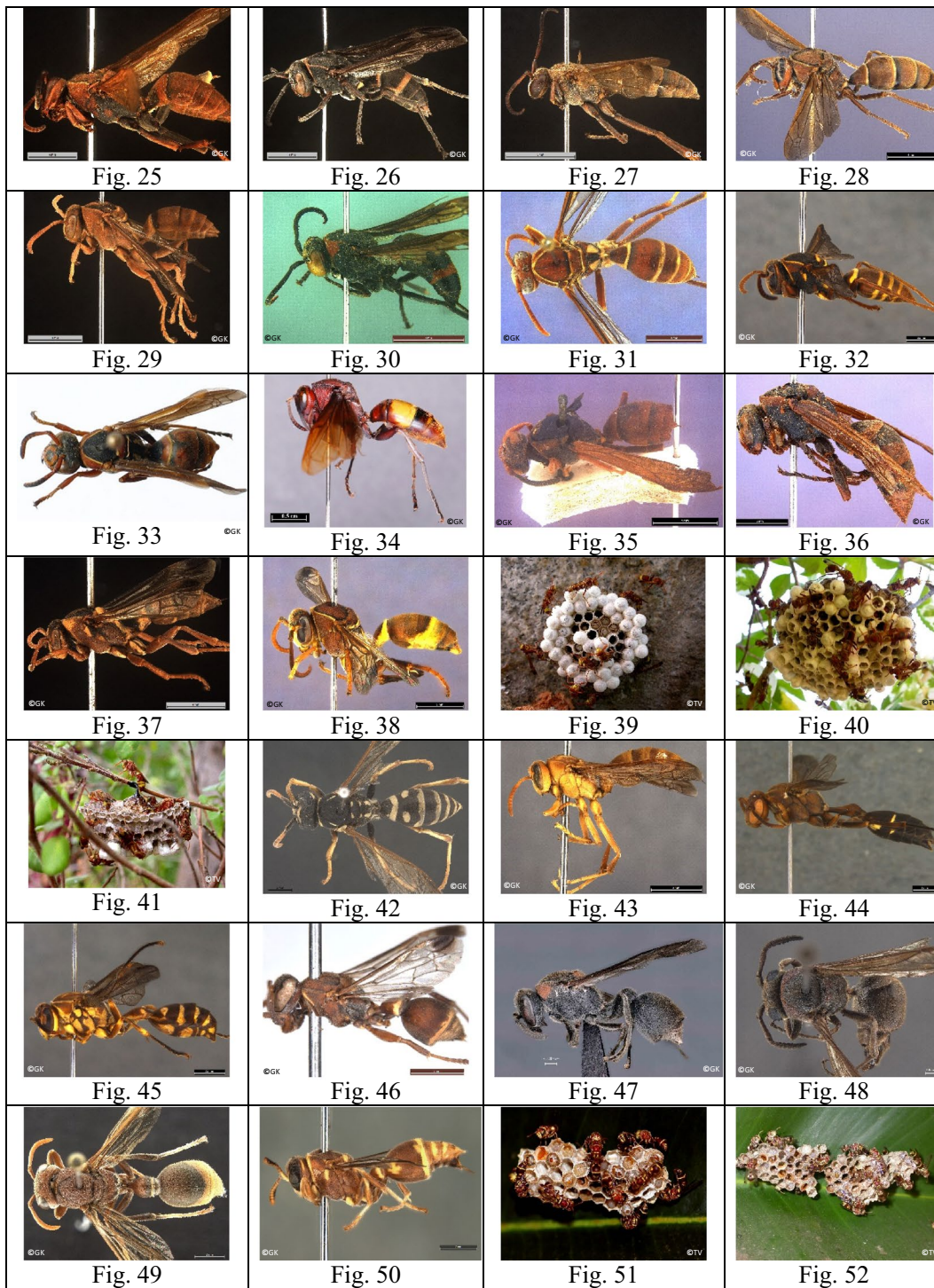


Figure 2: 25. *Polistes (Polistella) assamensis*, female. 26. *Polistes (Polistella) dawnae*, female. 27. *Polistes (Polistella) delhiensis*, male. 28. *Polistes (Polistella) khasianus*, female. 29. *Polistes (Polistella) latinis*, female. 30. *Polistes (Polistella) lepcha*, male. 31. *Polistes (Polistella) nigratarsis*, female. 32. *Polistes (Polistella) quadricingulatus*, female. 33. *Polistes (Polistella) rubellus*, female. 34. *Polistes (Polistella) sagittarius*, female. 35. *Polistes (Polistella) santoshae*, female paratype. 36. *Polistes (Polistella) similis*, female paratype. 37. *Polistes (Polistella) stigma novarae*, female. 38. *Polistes (Polistella) stigma tamulus*, female. 39 & 40. Nests of *Polistes stigma tamulus* on various substrata. 41. Nest of *Polistes stigma tamulus* showing single, thick pedicel (Location: Jalahally HMT area). 42. *Polistes (Polistes) biglumis*, female. 43. *Polistes (Polistes) indicus*, female. 44. *Parapolybia nodosa*, female. 45. *Parapolybia varia*, female. 46. *Ropalidia andamanensis*, female. 47. *Ropalidia bicolorata*, female. 48. *Ropalidia birmanica*, female. 49. *Ropalidia brevita*, female. 50. *Ropalidia cyathiformis*, female. 51. Single comb of *Ropalidia cyathiformis* nest. 52. *Ropalidia cyathiformis* nests with more than one comb.

26) *Polistes (Polistella) rubellus* Gusenleitner, 2006 (Fig. 2)

Polistes (Polistella) rubellus Guisenleitner, 2006: 684. Holotype female, Yuksom, Sikkim, India (STUTTGART).

Distribution: India: Arunachal Pradesh, Sikkim; Nepal^{64,66}.

27) *Polistes (Polistella) sagittarius* de Saussure, 1854 (Fig. 2)

Polistes sagittarius Saussure, 1853: 56. Female, “Indes Orientales, la Chine” (GENÈVE).

Distribution: India: Arunachal Pradesh, Assam, Delhi, Himachal Pradesh, Kerala, Manipur, Nagaland, Sikkim, Tripura, Uttarakhand, West Bengal; Bangladesh; Myanmar; Nepal. *Elsewhere*: China (including Hong Kong); Indonesia; Malaysia; Singapore; Thailand; Vietnam⁶⁴.

28) *Polistes (Polistella) santoshae* Das & Gupta, 1989 (Fig. 2)

Polistes santoshae Das & Gupta, 1989: 72. Holotype female, Shillong, Meghalaya, India (KOLKATA).

Distribution: India: Meghalaya, Sikkim; Bhutan; Nepal. *Elsewhere*: Vietnam⁶⁴.

29) *Polistes (Polistella) similis* Das & Gupta, 1989 (Fig. 2)

Polistes similis Das and Gupta, 1984: 413, nomen nudum.

Polistes similis Das and Gupta, 1989: 72. Holotype female, Shillong, Meghalaya, India (KOLKATA).

Distribution: India: Meghalaya⁶⁴.

30) *Polistes (Polistella) stigma* (Fabricius, 1793)

a) *Polistes (Polistella) stigma galathea* Petersen, 1987

Polistes stigma galathea Petersen, 1987: 239. Female, Little Nicobar, India (KØBENHAVN).

Distribution: India: Nicobar Islands⁶⁴.

b) *Polistes (Polistella) stigma novarae* de Saussure, 1867 (Fig. 2)

Polistes novarae Saussure, 1867: 19. Females & males, Tillanchang, Andaman & Nicobar Islands, India (VIENNA & GENÈVE).

Distribution: India: Nicobar Islands⁶⁴.

c) *Polistes (Polistella) stigma sauiensis* Petersen, 1987

Polistes stigma sauiensis Petersen, 1987: 240. Female, Sauí, Car Nicobar, India (VIENNA).

Distribution: India: Nicobar Islands⁶⁴.

d) *Polistes (Polistella) stigma tamulus* (Fabricius, 1798) (Fig. 2)

Vespa tamula Fabricius, 1798: 263. Female, “In India Orientali” (KØBENHAVN).

Polistes (Polistella) stigma tamula; Das & Gupta, 1984: 414.

Distribution: India: Bihar, Chhattisgarh, Delhi, Goa, Himachal Pradesh, Jharkhand, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Meghalaya, Odisha, Puducherry, Rajasthan, Sikkim, Tamil Nadu, Telangana, Uttarakhand, Uttar Pradesh, West Bengal; Pakistan; Sri Lanka. *Elsewhere*: Vietnam⁶⁴.

Nesting habits: It builds open nests with a single comb (Fig. 2) on many species of trees, plants, outside buildings, and under tiles of roofs and ceilings. Combs are attached to the substratum, mostly by a single pedicel (Fig. 2) and the nests are usually small to medium size (Personal observations).

31) *Polistes (Polistella) strigosus* Bequaert 1940

a) *Polistes (Polistella) strigosus atratus* Das & Gupta, 1989

Polistes (Polistella) strigosus atratus Das and Gupta, 1989: 81. Holotype female, Belonia, Tripura, India (KOLKATA).

Distribution: India: Assam, Bihar, Delhi, Manipur, Meghalaya, Sikkim, Tripura, Uttarakhand, West Bengal⁶⁴.

Nesting habits: This species is known to build small nests on leaves, grasses and small bushes close to the ground¹².

b) *Polistes (Polistella) strigosus strigosus* Bequaert, 1940

Polistes strigosus Bequaert, 1940: 269–272. Holotype female, Wong-Sa-Shui, China (CAMBRIDGE).

Distribution: India: Chhattisgarh, Madhya Pradesh, West Bengal. *Elsewhere*: China (including Hong Kong and Taiwan); Laos; Vietnam⁶⁴.

32) *Polistes (Polistella) associus* Kohl, 1898

Polistes associa Kohl, 1898: 89. Poros, Greece (VIENNA).

Distribution: India: Himachal Pradesh, Jammu & Kashmir; Pakistan. *Elsewhere*: Austria; Azerbaijan; China; Croatia; France; Greece; Hungary; Iran; Italy; Israel; Malta; Russia; Slovakia; southern Europe; Switzerland; Tajikistan; Turkey⁶⁴.

33) *Polistes (Polistella) biglumis* (Linnaeus, 1758) (Fig. 2)

Vespa biglumis Linnaeus, 1758: 573.

Polistes biglumis alpium Blüthgen, 1957: 163.
Distribution: Pakistan. *Elsewhere*: Europe; northern Africa; Turkey; Iran; Mongolia³⁶.
Nesting habits: *Polistes biglumis* builds nests mostly on stone substrate or wall¹⁴⁶. They studied the effect of climate on strategies of nest and body temperature regulation in paper wasps, *Polistes biglumis* and *Polistes gallicus*.

34) *Polistes (Polistella) dominula* (Christ, 1791)

Vespa dominula Christ, 1791: 229. Female, male, “Kronenberg an der Höh”, Germany (lost).

Distribution: India: Jammu & Kashmir; Pakistan. *Elsewhere*: Afghanistan; central and southern Europe; China; Cyprus; Germany; Iran; Israel; Jordan; Kazakhstan; Kyrgyzstan; Mongolia; Northern Africa; Russia; Syria; Tajikistan; Turkey; Turkmenistan; introduced into North America, South America, Australia; New Zealand⁶⁴.

35) *Polistes (Polistella) gallicus* (Linnaeus, 1767)

Vespa gallica Linnaeus, 1767: 949.

Polistes gallicus var. *mongolicus* du Buysson, 1911: 218.

Distribution: Pakistan. *Elsewhere*: Afghanistan; Armenia; Azerbaijan; China; Ethiopia; Iran; Israel; Mongolia; northern Africa; Russia; southern Europe; Turkey; Turkmenistan; Ukraine³⁶.

Nesting habits: The nesting ecology of this species is studied in Spain¹²⁰. They observed that this species nests on Asteraceae and their nest founding started from February to October. *P. gallicus* chose stone, concrete walls, window grills, and metal fences or door frames as nesting substrata¹⁴⁶.

36) *Polistes (Polistella) indicus* Stolfa, 1934 (Fig. 2)

Polistes indicus Stolfa, 1934: 47. Pakistan: Punjab: Salt Range: Khewra (KOLKATA).

Distribution: India: Uttar Pradesh; Pakistan. *Elsewhere*: Afghanistan; Iran; Iraq; Oman; United Arab Emirates⁶⁴.

37) *Polistes (Polistella) nimpha* (Christ, 1791)

Vespa nimpha Christ, 1791: 232. Female, “Kronenberg an der Höh”, Germany (lost).

Polistes nymphpha (!); Weyrauch, 1939: 145.

Distribution: India: Himachal Pradesh, Jammu & Kashmir; Pakistan. *Elsewhere*: Azerbaijan; central and southern Europe; China; Germany; Iran; Iraq; Israel; Jordan; Kazakhstan; Kyrgyzstan;

Mongolia; Northern Africa; Portugal (Madeiras); Russia; Turkey⁶⁴.

Nesting habits: The nesting ecology of *Polistes nimpha* is studied and found that this species nests on 30 species of plants in Poland⁹⁸.

Tribe Ropalidiini Bequaert, 1918

Genus *Belonogaster* de Saussure, 1853

Raphigaster Saussure, 1853: 12. Type species: *Vespa juncea* Fabricius 1781.

38) *Belonogaster indica* (de Saussure, 1853)

Raphigaster indicus Saussure, 1853: 17. Female, “Les Indes Orientales” (PARIS).

Belonogaster indica; Das & Gupta, 1984: 432.

Distribution: India: Maharashtra, Tamil Nadu⁶⁴.

39) *Belonogaster juncea juncea* (Fabricius, 1781)

Vespa juncea Fabricius, 1781: 468. Female, Africa Aequinoctiali (LONDON).

Belonogaster junceus; Smith, 1857: 93.

Distribution: India: Rajasthan. *Elsewhere*: Africa; Saudi Arabia⁶⁴.

Genus *Parapolybia* de Saussure, 1853

Parapolybia de Saussure, 1854: 207. Type species: *Polybia indica* de Saussure, 1854.

40) *Parapolybia escalerae* (Meade-Waldo, 1911)

Polybia escalerae Meade-Waldo, 1911: 109. Female (in subgenus *Parapolybia*), “Dupulán, Baktiari, S.W. Persia” (LONDON).

Parapolybia escalerae; von Schulthess, 1913: 153 (key), 159.

Distribution: Pakistan. *Elsewhere*: Iran; Turkey.

41) *Parapolybia fulvinerva* (Cameron, 1900)

Icaria fulvinerva Cameron, 1900: 504. Lectotype female, Khasia Hills, Meghalaya, India (OXFORD).

Parapolybia fulvinerva; Saito-Morooka et al., 2015: 222.

Distribution: India: Meghalaya⁶⁴.

42) *Parapolybia indica* (de Saussure, 1854)

Polybia indica de Saussure, 1854: 207. Holotype female, “La Chine” (PARIS).

Parapolybia indica; Schulthess, 1913: 153 & 154.

Parapolybia indica indica; van der Vecht, 1966: 26, 27.

Distribution: India: Arunachal Pradesh, Assam, Meghalaya; Myanmar; Nepal. *Elsewhere*: China (including Hong Kong and Taiwan); Indonesia; Japan; Korea; Laos; Thailand; Vietnam⁶⁴.

43) *Parapolybia nodosa* van der Vecht, 1966 (Fig. 2)

Parapolybia nodosa van der Vecht, 1966: 39, 40. Holotype female, "Pilam, Formosa" (Taiwan) (LEIDEN).

Distribution: India: Assam, Delhi, Haryana, Meghalaya; Bhutan; Myanmar; Nepal. *Elsewhere*: China (including Hong Kong and Taiwan); Laos; Thailand; Vietnam⁶⁴.

44) *Parapolybia tinctipennis* (Cameron, 1900)

Icaria tinctipennis Cameron, 1900: 503. Female, Khasia Hills, Meghalaya, India (OXFORD).

Parapolybia tinctipennis; Saito-Morooka et al., 2015: 223.

Distribution: India: Assam, Arunachal Pradesh, Meghalaya. *Elsewhere*: China; Laos; Vietnam⁶⁴.

45) *Parapolybia varia* (Fabricius, 1787) (Fig. 2)

Vespa varia Fabricius, 1787: 293. China (KØBENHAVN).

Distribution: India: Arunachal Pradesh, Assam, Delhi, Himachal Pradesh, Manipur, Meghalaya, Mizoram, Punjab, Sikkim, Uttarakhand, Uttar Pradesh, West Bengal; Bhutan; Myanmar; Nepal. *Elsewhere*: China (including Hong Kong and Taiwan); Indonesia; Japan; Korea; Malaysia; Philippines; Thailand; Vietnam⁶⁴.

Genus *Polybioides* du Buysson, 1913

Polybioides du Buysson, 1913: 299. Type species: "*Polybioides tabidus* (F.)" [= *Vespa tabida* Fabricius, 1781].

46) *Polybioides gracilis* van der Vecht, 1966

Polybioides gracilis van der Vecht, 1966: 13 (key), 19. Female, "Tenasserim: Ataran Valley" (LONDON).

Distribution: Myanmar. *Elsewhere*: Malay Peninsula; Vietnam.

Genus *Ropalidia* Guérin-Méneville, 1831

Ropalidia Guérin-Méneville, 1831: 9. Type species: *Ropalidia maculiventris* Guérin-Méneville, 1831.

Anthreneida White, 1841: 321. Type species: *Anthreneida coronata* White, 1841 (= *Vespa sumatrae* Weber, 1801).

Icaria de Saussure, 1853: 22. Type species: "*Icaria maculiventris* (Guer.)" (= *Ropalidia maculiventris* Guérin-Méneville, 1831).

Paraicaria Gribodo, 1892 (1891): 248. Type species: *Paraicaria bicolor* Gribodo, 1892 (= *Ropalidia bicolorata* van der Vecht, 1962).

Icariastrum Dalla Torre, 1904: 72. Type species: *Icaria opulenta* Smith, 1857.

Icarielia Dalla Torre, 1904: 72. Type species: *Icaria flavopicta* Smith, 1857.

Icariola Dalla Torre, 1904: 72. Type species: *Icaria gregaria* de Saussure, 1853.

Polistratus Cameron, 1906: 59. Type species: *Polistratus cariniscutis* Cameron, 1906 (= *Icaria brunnea* Smith, 1858).

47) *Ropalidia andamanensis* Das and Gupta, 1989 (Fig. 2)

Ropalidia (*Anthreneida*) *andamanensis* Das and Gupta, 1989: 139. Holotype female, Port Blair, Andaman Islands, India (KOLKATA).

Distribution: India: Andamans⁶⁴.

48) *Ropalidia bicolorata* van der Vecht, 1962 (Fig. 2)

Paraicaria bicolor Gribodo, 1892: 249. Female, Chan Yoma (Myanmar) (GENOVA).

Ropalidia bicolorata bicolorata van der Vecht, 1962: 38, 39.

Distribution: India: Assam, Manipur, Meghalaya, Mizoram, Nagaland, Tripura; Myanmar. *Elsewhere*: China; Laos; Malaysia; Thailand; Vietnam⁶⁴.

49) *Ropalidia birmanica* van der Vecht, 1962 (Fig. 2)

Ropalidia taiwana birmanica van der Vecht, 1962: 23. Holotype male, "Northeast Burma, Sadon" (Myanmar) (STOCKHOLM).

Ropalidia birmanica; Kojima et al., 2007: 382.

Distribution: India: Mizoram; Myanmar. *Elsewhere*: China; Vietnam⁶⁴.

50) *Ropalidia brevita* Das & Gupta, 1989 (Fig. 2)

Ropalidia (*Antreneida*) *brevita* Das and Gupta, 1989: 110, 121, 163. Holotype male, Delhi, India (KOLKATA).

Distribution: India: Arunachal Pradesh, Assam, Chhattisgarh, Delhi, Goa, Gujarat, Haryana, Himachal Pradesh, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Odisha, Rajasthan,

Sikkim, Tamil Nadu, Telangana, Uttarakhand, Uttar Pradesh, West Bengal; Pakistan⁶⁴.

51) *Ropalidia colorata* van der Vecht, 1941

Ropalidia colorata colorata van der Vecht, 1941: 111, 151. Female, Peshawar, Pakistan (LONDON).

Distribution: India: Himachal Pradesh, Uttarakhand; Pakistan⁶⁴.

52) *Ropalidia cyathiformis* (Fabricius, 1804) (Fig. 2)

Eumenes cyathiformis Fabricius, 1804: 289. Holotype female, “Java” (KØBENHAVN).

Ropalidia cyathiformis; van der Vecht, 1941: 104, 112, 158.

Distribution: India: Andhra Pradesh, Arunachal Pradesh, Assam, Bihar, Chhattisgarh, Goa, Gujarat, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Rajasthan, Telangana, Uttarakhand, West Bengal; Myanmar; Nepal; Pakistan; Sri Lanka. *Elsewhere*: China; Indonesia; Malaysia; Philippines; Thailand; Vietnam^{64,80}.

Nesting habits: This species of *Ropalidia* nests on leaves of many trees, plants, shrubs, on walls, windows, ceilings, tiles, and rocks etc. *R. cyathiformis* makes nests with a single comb (Fig. 2) attached to the substratum at 90 degrees; rarely a single colony occupies multiple combs (Fig. 2 & Fig. 3).

Remarks: It shows an enormous amount of variation in its colour pattern, especially in black markings, within and across colonies. Males are as usual lighter and more yellowish than females (Fig. 3). Consistently, males lack the typical mark on the clypeal area as observed in clypeal area of females (Fig. 3). Antennae of males are 13 segmented, the segments are with well-defined tyloids and the last antennal segment is slightly curved as seen in Fig. 3. (Personal observation). An earlier study looked at the social organization in this species in detail⁶² and few other studies provided notes on its natural history⁹⁴ and behaviour^{151,152}.

Variations within species (in colour pattern): Individuals collected from most of the nests are darker than the typical form described earlier^{45,154}. In darker forms, there are narrow/broad black marks on mesonotum, meta sternum, and a black dot above their antennae, scutellum, post-scutellum, and sides of propodeum, first and the second gastral segments. The lighter forms agree with the typical form, while the darker ones agree with the colour variation of this species as mentioned in an earlier publication⁴⁵ (Personal observations).

53) *Ropalidia fasciata* (Fabricius, 1804) (Fig. 3)

Eumenes fasciata Fabricius, 1804: 290. Syntype males, “Java” (KØBENHAVN).

Ropalidia fasciata; van der Vecht, 1959a [1958]: 245.

Distribution: India: Arunachal Pradesh, Assam, Delhi, Maharashtra, Meghalaya, Odisha, Sikkim, Tamil Nadu, Tripura, Uttarakhand, Uttar Pradesh; Bhutan; Myanmar; Nepal; Pakistan; Sri Lanka. *Elsewhere*: China (including Hong Kong and Taiwan); Japan; Indonesia; Laos; Malaysia; Philippines; Thailand; Timor; Vietnam⁶⁴.

54) *Ropalidia hongkongensis* (de Saussure, 1854) (Fig. 3)

Icaria hongkongensis de Saussure, 1854: 239. Female, “La Chine, Hong Kong” (LONDON).

Ropalidia hongkongensis juncta van der Vecht, 1941: 141. Holotype female, “Tjiboerial near Buitenzorg, W. Java” (LEIDEN).

Distribution: India: Assam, Manipur, Meghalaya, Nagaland; Myanmar. *Elsewhere*: China (including Hong Kong); Indonesia; Laos; Vietnam⁶⁴.

55) *Ropalidia jacobsoni* (du Buysson, 1908) (Fig. 3)

Icaria jacobsoni du Buysson, 1908: 123. Lectotype female, “aux environs de Batavia [=Jakarta]” (LEIDEN).

Ropalidia jacobsoni jacobsoni: Das and Gupta, 1984: 418.

Distribution: India: Arunachal Pradesh, Assam, Chhattisgarh, Delhi, Goa, Gujarat, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Meghalaya, Nagaland, Rajasthan, Tamil Nadu, Uttarakhand, Uttar Pradesh, West Bengal; Bhutan; Myanmar. *Elsewhere*: Indonesia⁶⁴.

Nesting habits: This is another *Ropalidia* species with very wide distribution. It makes nest on leaves of many trees, shrubs, fences and many similar substrata (Fig. 3). In many cases, the nests camouflage well with the surroundings and are tough to notice. The nests are unique with only two columns, built vertically and usually a single colony occupies single comb, but occasionally colonies occupy many combs which are placed very close together (Fig. 3). The combs are mostly attached at about 45° to the substratum and the combs hang from the substratum downwards. In few cases, the combs are attached at about 90° to the substratum also (Personal observations).

Remarks: In this species, there exists apparent variation in colour pattern both in males (Fig. 3) and females, even within a colony (Fig. 3). Males

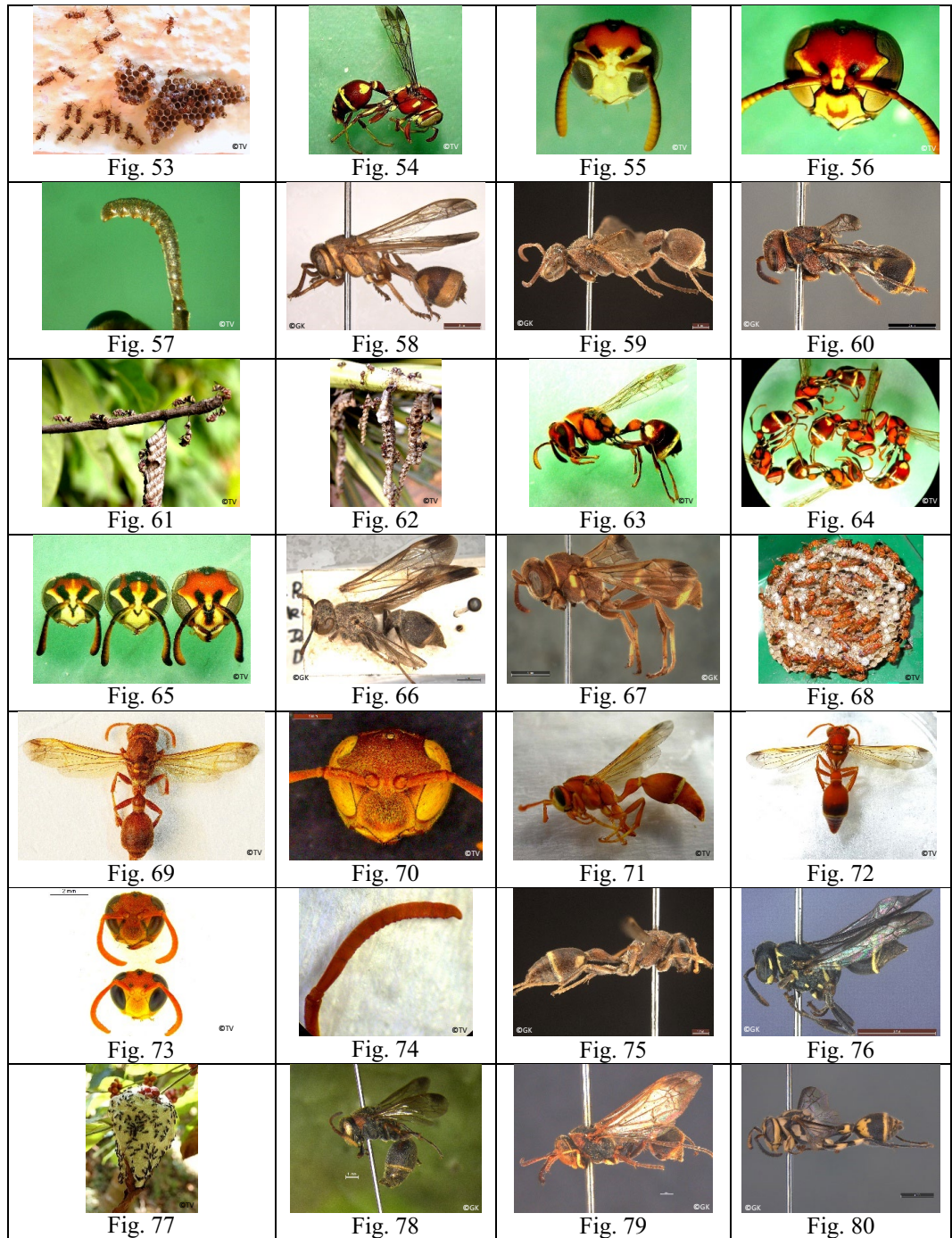


Figure 3: 53. *Ropalidia cyathiformis* nests with more than one comb. 54. *Ropalidia cyathiformis*, male. 55. *Ropalidia cyathiformis*, male, head frontal view showing yellow clypeus. 56. *Ropalidia cyathiformis*, female, head frontal view showing typical mark on clypeus. 57. *Ropalidia cyathiformis*, male antenna showing tyloids. 58. *Ropalidia fasciata*, female. 59. *Ropalidia hongkongensis*, female. 60. *Ropalidia jacobsoni*, female. 61. A typical nesting site of *Ropalidia jacobsoni*. 62. Nest of a single colony of *Ropalidia jacobsoni*, with multiple combs which are built very close to each other. 63. *Ropalidia jacobsoni*, male. 64. *Ropalidia jacobsoni*, females showing variations in colour patterns. 65. *Ropalidia jacobsoni*, head frontal view of male and female, showing clypeus. 66. *Ropalidia kasaragodensis*, female holotype. 67. *Ropalidia marginata*, female. 68. *Ropalidia marginata* nest. 69. *Ropalidia marginata*, female, dorsal view. 70. *Ropalidia marginata*, female, head frontal view showing broad mark on clypeus. 71. *Ropalidia marginata*, male, profile. 72. *Ropalidia marginata*, male, dorsal view. 73. *Ropalidia marginata*, female & male, head frontal view showing differences in markings on clypeus. 74. *Ropalidia marginata*, male, antenna showing tyloids. 75. *Ropalidia mathematica*, female. 76. *Ropalidia montana*, female. 77. *Ropalidia montana* nest on coffee plant (Kalpetta, Wayanad). 78. *Ropalidia narendrani*, female. 79. *Ropalidia nigrita*, female paratype. 80. *Ropalidia ornaticeps*, female.

are as usual with yellow clypeus, but occasionally with tint of black markings below the antennal sockets (Fig. 3). Whereas the clypeus of females shows elongated, thick black marking medially (Personal observations).

Variations in colour pattern-within species: The black markings on various parts of thorax, like, pronotum, mesonotum, metanotum, propodeum and ventral side of body, frontal area are darker than in typical forms. Even in the same colony, there are variations in colour pattern to certain extent (Black markings). Similarly, black markings on vertex vary a lot; narrow to broad around ocelli, in some the black mark around ocelli spreads the whole space between the eyes. In most of the nests, individuals are darker than the typical form, within the same nest both darker and lighter forms are observed. However, other characters in male are consistent within and across colonies (Personal observations).

56) *Ropalidia kasaragodensis* Lambert & Narendran, 2005 (Fig. 3)

Ropalidia indica Lambert & Narendran in Lambert *et al.*, 2005: 1921. Holotype female, Kasargod, Kerala, India (KOZHICODE).

Ropalidia kasaragodensis; replacement name by Kojima *et al.*, 2007: 382.

Distribution: India: Kerala⁶⁴.

57) *Ropalidia marginata* (Lepeletier, 1836) (Fig. 3)

Epipona marginata Lepeletier, 1836: 541. "Inde" (TORINO).

Ropalidia marginata; Dover and Rao, 1922: 244.

Distribution: India: Andhra Pradesh, Chhattisgarh, Goa, Gujarat, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Odisha, Punjab, Rajasthan, Tamil Nadu, Telangana, Uttarakhand, Uttar Pradesh, West Bengal; Myanmar; Pakistan; Sri Lanka. **Elsewhere:** Australia; China (including Hong Kong); Indonesia; Japan; Malaysia; Mariana Islands; Papua New Guinea; Palau; Philippines; Vietnam⁶⁴.

Nesting habits: The electric boxes are the most preferred nesting place for *R. marginata*. Other nesting sites are windowpanes, below tiles, pipes, abandoned furniture and buildings, occasionally walls and many bushy plants. In rare instances at least, it makes nests in crevices of buildings and walls. *R. marginata* colonies usually built a single comb of varying sizes and shapes (Fig. 3). But very rarely a colony occupies more than one comb simultaneously. Wherever they are, whatever be the form and size, the combs are almost always

attached to the substratum by pedicel at an angle of roughly 90°, such that the combs are mostly oriented in a vertical plane with the substratum, attached mostly by a single pedicel, which is thin in small nests, whereas it is very thick in larger, older nests (Personal observations).

Remarks: Though females (Fig. 3) and males look similar in size and shape, the males are distinct (Fig. 3) with yellowish clypeus and 13 segmented antennae (Fig. 3). Antennae of males are with tyloids (Fig. 3) as in males of many other species of *Ropalidia*. Intraspecific variations are insignificant, compared to that in other species of *Ropalidia* (Personal observations).

58) *Ropalidia mathematica* (Smith, 1860) (Fig. 3)

Polybia mathematica Smith, 1860: 90. Female, "Makassar" (OXFORD).

Ropalidia mathematica mathematica; van der Vecht 1941: 110 & 130.

Distribution: India: Kerala, Maharashtra, Meghalaya, Tripura, Uttarakhand. **Elsewhere:** China; Indonesia; Laos; Thailand; Timor; Vietnam⁶⁴.

59) *Ropalidia montana* Carl, 1934 (Fig. 3)

Icaria montana Carl, 1930: 22, nomen nudum. *Ropalidia montana* Carl, 1934: 675. Kannur, Kerala, India (GENÈVE).

Distribution: India: Karnataka, Kerala, Tamil Nadu⁶⁴.

Nesting habits: *R. montana*, endemic to Western Ghats, is seen mostly in and around forest areas and among thick vegetations. It builds nests with multiple layers of combs covered with an envelope (Fig. 3).

60) *Ropalidia narendrani* Shareef, Kishore & Girish Kumar, 2015 (Fig. 3)

Ropalidia narendrani Shareef, Kishore & Girish Kumar in Mohammed Shareef *et al.*, 2015: 6837. Holotype female, Periyar Tiger Reserve, Kerala, India (KOLKATA).

Distribution: India: Kerala⁶⁴.

61) *Ropalidia nigrita* Das & Gupta, 1989 (Fig. 3)

Ropalidia (Anthreneida) nigrita Das and Gupta, 1989: 130. Holotype male, Moirang, Manipur, India (KOLKATA).

Distribution: India: Manipur; Nepal. **Elsewhere:** Vietnam⁶⁴.

62) *Ropalidia ornaticeps* (Cameron, 1900) (Fig. 3)

Icaria ornaticeps Cameron, 1900: 496. Female, Khasia Hills, Meghalaya, India (OXFORD & LONDON).

Ropalidia ornaticeps; Yoshikawa et al., 1969: 167.

Distribution: India: Arunachal Pradesh, Assam, Meghalaya, Mizoram, Sikkim, Tripura; Bhutan; Myanmar. *Elsewhere*: Cambodia; China; Laos; Malaysia; Thailand; Vietnam⁶⁴.

63) *Ropalidia rufocollaris* (Cameron, 1900) (Fig. 4)

Icaria rufocollaris Cameron, 1900: 497. Holotype female, Khasia Hills, Meghalaya, India (LONDON).

Ropalidia rufocollaris atrata van der Vecht, 1941: 139.

Distribution: India: Arunachal Pradesh, Assam, Chhattisgarh, Kerala, Madhya Pradesh, Meghalaya, Mizoram, Nagaland, Sikkim, Tamil Nadu, Tripura, Uttarakhand, West Bengal; Bhutan; Myanmar. *Elsewhere*: China: Tibet; Laos; Thailand; Vietnam⁶⁴.

64) *Ropalidia rufoplagiata* (Cameron, 1905) (Fig. 4)

Icaria rufoplagiata Cameron, 1905: 71. Lectotype female, "Tjandi near Semarang" (AMSTERDAM).

Ropalidia rufoplagiata; van der Vecht, 1941: 111, 165.

Distribution: India: Andaman & Nicobar Islands, Karnataka, Kerala, Maharashtra, Meghalaya, Uttarakhand; Bhutan; Myanmar. *Elsewhere*: Indonesia; Malaysia; Thailand; Timor; Vietnam⁶⁴.

Nesting habits: This species makes roughly oval to moderately elongated nests (Fig. 4). While some nests are rectangular and can be very large in size (Fig. 4). The nests are usually of single comb, very rarely of more than one comb. All combs are attached to the substratum, roughly at an angle of 90°, to make the combs parallel to the substratum, as in *R. marginata* and *R. cyathiformis* nests. It inhabits windowpane, stone walls, pillars, and corners of buildings. The nests are quite conspicuous, but when it is built in windowpanes it is hidden inside the grooves and easily overlooked. Rarely at least, it builds nest in enclosed boxes of different dimensions. Often, there is more than one pedicel, especially for large colonies (Personal observations).

Remarks: The females and males of this species exhibit intraspecific variations to a larger degree (Fig. 4). A strong dark variant form of the common species is also present in Karnataka

(Fig. 4) (Earlier known as *R. rufoplagiata grave-lyi*, now synonymised under *R. rufoplagiata*⁹⁷. Even in the same colony, there is lighter and darker forms (Personal observations). Males are lighter with 13 segmented antennae.

65) *Ropalidia sahyadrica* Kishore, Shareef & Girish Kumar, 2014 (Fig. 4)

Ropalidia sahyadrica Kishore, Shareef & Girish Kumar in Lambert et al., 2014: 235-236. Holotype male, Muthappanpuzha, Kerala, India (KOLKATA).

Distribution: India: Kerala⁶⁴.

66) *Ropalidia santoshae* Das & Gupta, 1989 (Fig. 4)

Ropalidia (Antreneida) santoshae Das & Gupta, 1989: 123. Holotype male, Shillong, Meghalaya, India (KOLKATA).

Distribution: India: Arunachal Pradesh, Meghalaya, Sikkim, West Bengal; Bhutan. *Elsewhere*: China⁶⁴.

67) *Ropalidia scitula* (Bingham, 1897) (Fig. 4)

Icaria scitula Bingham, 1897: 387, 392. Female, Rangit Velley, Sikkim, India (LONDON).

Ropalidia (Icarielia) scitula; van der Vecht, 1941: 142.

Distribution: India: Arunachal Pradesh, Manipur, Meghalaya, Mizoram, Sikkim, West Bengal; Myanmar. *Elsewhere*: China; Laos; Thailand⁶⁴.

68) *Ropalidia sculpturata* Gusenleitner, 2001

Ropalidia sculpturata Gusenleitner, 2001: 655. Holotype female, "Nepal: Annapurna, Kimal, Lumle" (LINZ).

Distribution: Nepal⁹⁷.

69) *Ropalidia spatulata* van der Vecht, 1962 (Fig. 4)

Ropalidia marginata indica van der Vecht, 1941: 121.

Ropalidia spatulata van der Vecht, 1962: 9. Male, Walayar forest, Kerala, India (LEIDEN).

Distribution: India: Kerala, Rajasthan, Tamil Nadu, Telangana; Myanmar; Pakistan⁶⁴.

Nesting habits: This species nests on tree branches, walls, abandoned buildings, below tiles etc. It builds open nests with single comb of various sizes and shapes (Fig. 4).

Remarks: This species shows elaborate black and lavish yellow markings. The males are little lighter in colour and the clypeus is with partial yellow markings in the mid anterior area.

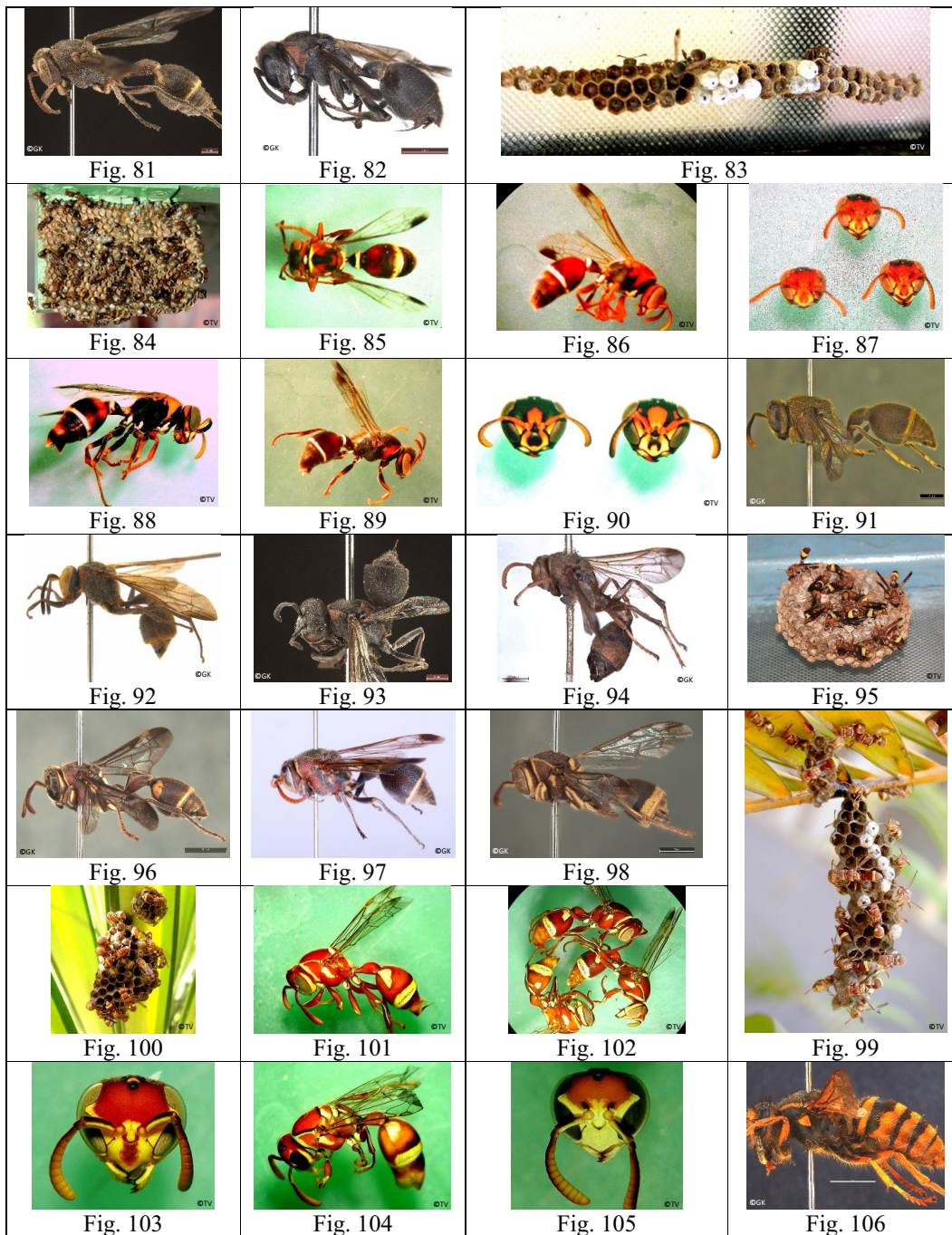


Figure 4: 81. *Ropalidia rufocollaris*, female. 82. *Ropalidia rufoplagiata*, female. 83, 84. *R. rufoplagiata*, nests of various shapes and sizes. 85. *R. rufoplagiata*, female, dorsal view. 86. *R. rufoplagiata*, female, profile. 87. *R. rufoplagiata*, female, head frontal view showing intraspecific variation in colour pattern on clypeus. 88–90. *R. rufoplagiata*, females showing variations in black markings on body and clypeus. 91. *Ropalidia sahyadrica*, female. 92. *Ropalidia santhoshae*, male. 93. *Ropalidia scitula*, female. 94. *Ropalidia spatulata*, male holotype. 95. Nest of *R. spatulata* (Walayar, Palghat). 96. *Ropalidia stigma*, female. 97. *Ropalidia tamila*, male. 98. *Ropalidia variegata*, female. 99. *R. variegata* nest on Palm leaf (Location: Majestic area, Bangalore). 100. *R. variegata* nest, two combs of different size and shape (Location: Majestic area, Bangalore). 101, 102. *R. variegata*, females, profile. 103. *R. variegata*, female, head frontal view showing clypeus. 104. *R. variegata*, male, profile. 105. *R. variegata*, male, head frontal view showing clypeus. 106. *Dolichovespula intermedia*, female

70) *Ropalidia stigma* (Smith, 1858) (Fig. 4)
Polybia stigma Smith, 1858: 114. Male, Sarawak, Malaysia (OXFORD).

Ropalidia stigma stigma; van der Vecht, 1941: 110, 126.

Distribution: India: Arunachal Pradesh, Assam, Chhattisgarh, Goa, Himachal Pradesh, Jharkhand, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Manipur, Meghalaya, Mizoram, Nagaland, Odisha, Sikkim, Tripura, Uttarakhand, West Bengal; Bhutan; Myanmar; Nepal; Sri Lanka. *Elsewhere*: China (including Hong Kong); Indonesia; Laos; Malaysia; Philippines; Singapore; Thailand; Vietnam⁶⁴.

71) *Ropalidia sumatrae* (Weber, 1801)

Vespa sumatrae Weber, 1801: 103. "Sumatra" (? BERLIN).

Ropalidia sumatrae van der Vecht, 1941: 104.

Distribution: India: West Bengal; Myanmar. *Elsewhere*: China; Indonesia; Malaysia; Singapore; Thailand⁶⁴.

72) *Ropalidia tamila* Gusenleitner, 2004 (Fig. 4)

Ropalidia tamila Gusenleitner, 2004: 1089. Holotype female, Tamil Nadu, India (LINZ).

Distribution: India: Goa, Kerala, Tamil Nadu⁶⁴.

73) *Ropalidia variegata* (Smith, 1852) (Fig. 4)

Epipona variegata Smith, 1852a: 48. Female, Pune, Maharashtra, India (LEIDEN).

Ropalidia variegata; Bequaert, 1918: 247.

Distribution: India: Andhra Pradesh, Bihar, Chhattisgarh, Delhi, Gujarat, Haryana, Jammu & Kashmir, Karnataka, Kerala, Madhya Pradesh, Maharashtra, Punjab, Rajasthan, Tamil Nadu, Telangana, Uttarakhand, Uttar Pradesh, West Bengal; Myanmar; Nepal; Pakistan. *Elsewhere*: China; Indonesia; Malaysia⁶⁴.

Nesting habits: *R. variegata* inhabits diverse habitats and builds round to elongated nests on tree leaves, branches and below ceilings etc. (Fig. 4). The nests are similar in shape to that of *R. cyathiformis*. In many cases, combs are attached to the substratum at 90° and the combs hang from the substratum as in the case of *R. jacobsoni*, whereas several nests are attached to the substratum as in *R. marginata* and *R. cyathiformis*. Interestingly, many colonies use multiple small combs simultaneously, which are made very close to each other. But the number of combs observed in any nest at any given point of time is usually not more than 3 in those species, but the number of

combs in *R. variegata* nests may vary from 1–30 (Personal observations).

Remarks: The females (Fig. 4) and males of this species are bright ferruginous with lots of yellow and very little black markings. Males are as usual with bright yellow clypeus and antennae are without tyloids (Fig. 4). This species is very close to *R. cyathiformis* in size and morphology. This species comes to *R. variegata variegata* in Das and Gupta's key and agrees with the earlier descriptions^{45,54} (Personal observations).

Subfamily Vespinae

Genus *Dolichovespula* Rohwer, 1916

Vespula (*Dolichovespula*) Rohwer, 1916: 642. Type species: *Vespa maculata* Linnaeus, 1763.

Pseudovespula Bischoff, 1930: 346. Type species: "*Pseudovespula adulterina* Buysson" (= *Vespa norwegica* var. *adulterina* du Buysson, 1905 (1904)).

Boreovespula Bluthgen, 1943: 149. Type species: "*Dolichovespula norwegica* (Fabricius)" (= *Vespa norwegica* Fabricius, 1781).

Metavespula Bluthgen, 1943: 149. Type species: "*Dolichovespula silvestris* (Scopoli)" (= *Vespa silvestris* Scopoli, 1763).

74) *Dolichovespula flora* Archer, 1987

Dolichovespula flora Archer, 1987: 27. Female, "BURMA, Adung Valley" (LONDON); also from China.

Distribution: Myanmar. *Elsewhere*: China³⁸.

75) *Dolichovespula intermedia* (Birula, 1930) (Fig. 4)

Vespula silvestris intermedia Birula, 1930: 330, 331. Lectotype female, East Bukhara, Uzbekistan (ST PETERSBURG).

Dolichovespula asiatica Archer, 1981a: 187, 189.

Distribution: India: Himachal Pradesh, Jammu & Kashmir; Pakistan. *Elsewhere*: Afghanistan; China; Kazakhstan; Kyrgyzstan; Mongolia; Russia; Tajikistan; Turkmenistan; Uzbekistan⁶⁴.

76) *Dolichovespula lama* (du Buysson, 1903)

Vespa lama du Buysson, 1903: 175. Holotype female, Sikkim, India (PARIS).

Dolichovespula nyalamensis Lee, 1986: 195, 197.

Distribution: India: Sikkim, Uttarakhand; Bhutan; Nepal. *Elsewhere*: China⁶⁴.

77) *Dolichovespula silvestris* (Scopoli, 1763)

Vespa sylvestris Scopoli, 1763: 309. “Carnioliae” [Slovenia] (destroyed?).

Dolichovespula xinjiangensis Lee, 1986: 195, 199.

Distribution: India: Jammu & Kashmir; Pakistan. *Elsewhere*: Afghanistan; Albania; Armenia; Austria; Belarus; Belgium; Bulgaria; China; Czech Republic; Denmark; Finland; France; Georgia; Germany; Greece; Hungary; Iran; Ireland; Italy; Japan; Kazakhstan; Kyrgyzstan; Luxembourg; Macedonia; Mongolia; Morocco; Netherlands; North Korea; Norway; Poland; Portugal; Romania; Russia; Slovakia; Slovenia; Spain; Sweden; Switzerland; Syria; Tajikistan; Turkey; Ukraine; United Kingdom; Uzbekistan⁶⁴.

78) *Dolichovespula xanthicincta* Archer, 1981

Dolichovespula pacifica xanthicincta Archer, 1981: 341, 343. Female [male = female], “CHINA-TIBET BORDER, near Tang Gu, 4300 m” (WASHINGTON); also from Xizang; Myanmar.

Distribution: Bhutan; Myanmar. *Elsewhere*: China³⁸.

Genus *Provespa* Ashmead, 1903

Provespa Ashmead, 1903: 182. Type species: *Vespa dorylloides* de Saussure, 1854 [= *Vespa anomala* de Saussure, 1854].

79) *Provespa barthelemyi* (du Buysson, 1905) (Fig. 5)

Vespa barthelemyi du Buysson, 1905 (1904): 492, 618. Lectotype female, Phnom Penh, Cambodia (PARIS).

Provespa barthelemyi; van der Vecht, 1936: 165.

Distribution: India: Assam, Arunachal Pradesh, Manipur, Meghalaya, Nagaland, Tripura, Mizoram, Sikkim, West Bengal; Bangladesh; Bhutan; Myanmar. *Elsewhere*: Cambodia; China; Laos; Malaysia; Thailand; Vietnam⁶⁴.

Genus *Vespa* Linnaeus, 1758

Vespa Linnaeus, 1758: 343, 572. Type species: “*Vespa crabro*, Fab.” (= *Vespa crabro* Linnaeus, 1758).

Macrovespa Dalla Torre, 1904: 64. Type species: *Vespa crabro* Linnaeus, 1758.

Nyctovespa van der Vecht, 1959b: 210. Type species: *Vespa binghami* du Buysson, 1905 (1904).

Nesting habits: The genus *Vespa* known as “hornets” inhabits diverse habitats and builds nests on tree branches, both outside and inside of buildings, windowpanes etc. (Fig. 5). All species

make enclosed nests with multiple combs inside (Fig. 5).

80) *Vespa affinis* (Linnaeus, 1764) (Fig. 5)

Apis affinis Linnaeus, 1764: 417. Female, “in Calidis regionibus” (Oriental Region) (UPPSALA).

Vespa affinis affinis; Bequaert, 1936: 347.

Distribution: India: Arunachal Pradesh, Assam, Bihar, Himachal Pradesh, Karnataka, Kerala, Maharashtra, Meghalaya, Nagaland, Sikkim, Tamil Nadu, Tripura, Uttarakhand, Uttar Pradesh, West Bengal; Bangladesh; Bhutan; Myanmar; Nepal; Sri Lanka. *Elsewhere*: China; Cambodia; Indonesia; Laos; Malaysia; Singapore; Thailand; Vietnam⁶⁴.

Nesting habits: *Vespa affinis* inhabits a wide variety of habitats and builds nests of various sizes, depending on the size of the colony. On the campus of the Indian Institute of Science, this species is found nesting on branches of many trees, both tall and short, outside active and abandoned buildings etc.

81) *Vespa analis* Fabricius, 1775 (Fig. 5)

Vespa analis Fabricius, 1775: 363. Probably Java (LONDON).

Distribution: India: Arunachal Pradesh, Assam, Jammu & Kashmir, Meghalaya, Sikkim, Tamil Nadu, Uttarakhand, West Bengal; Bhutan; Myanmar; Nepal; Pakistan. *Elsewhere*: China (including Taiwan); Indonesia; Japan; Laos; Malaysia; Russia; Singapore; South Korea; Thailand; Vietnam⁶⁴.

Nesting habits: This species is known to nest on hill sides in forest areas⁸.

82) *Vespa basalis* Smith, 1852 (Fig. 5)

Vespa basalis Smith, 1852a: 46. Female, Nepal (LONDON).

Distribution: India: Arunachal Pradesh, Assam, Himachal Pradesh, Meghalaya, Mizoram, Odisha, Punjab, Sikkim, Uttarakhand, Uttar Pradesh, West Bengal; Bhutan; Myanmar; Nepal; Pakistan. *Elsewhere*: China (including Taiwan); Indonesia; Laos; Thailand; Vietnam⁶⁴.

83) *Vespa bicolor* Fabricius, 1787 (Fig. 5)

Vespa bicolor Fabricius, 1787: 288. “in China D. Pflug” (KØBENHAVN).

Distribution: India: Arunachal Pradesh, Assam, Manipur, Meghalaya, Sikkim, Uttarakhand, West Bengal; Bhutan; Myanmar; Nepal. *Elsewhere*: Cambodia; China (including Taiwan); Japan; Laos; Thailand; Vietnam⁶⁴.

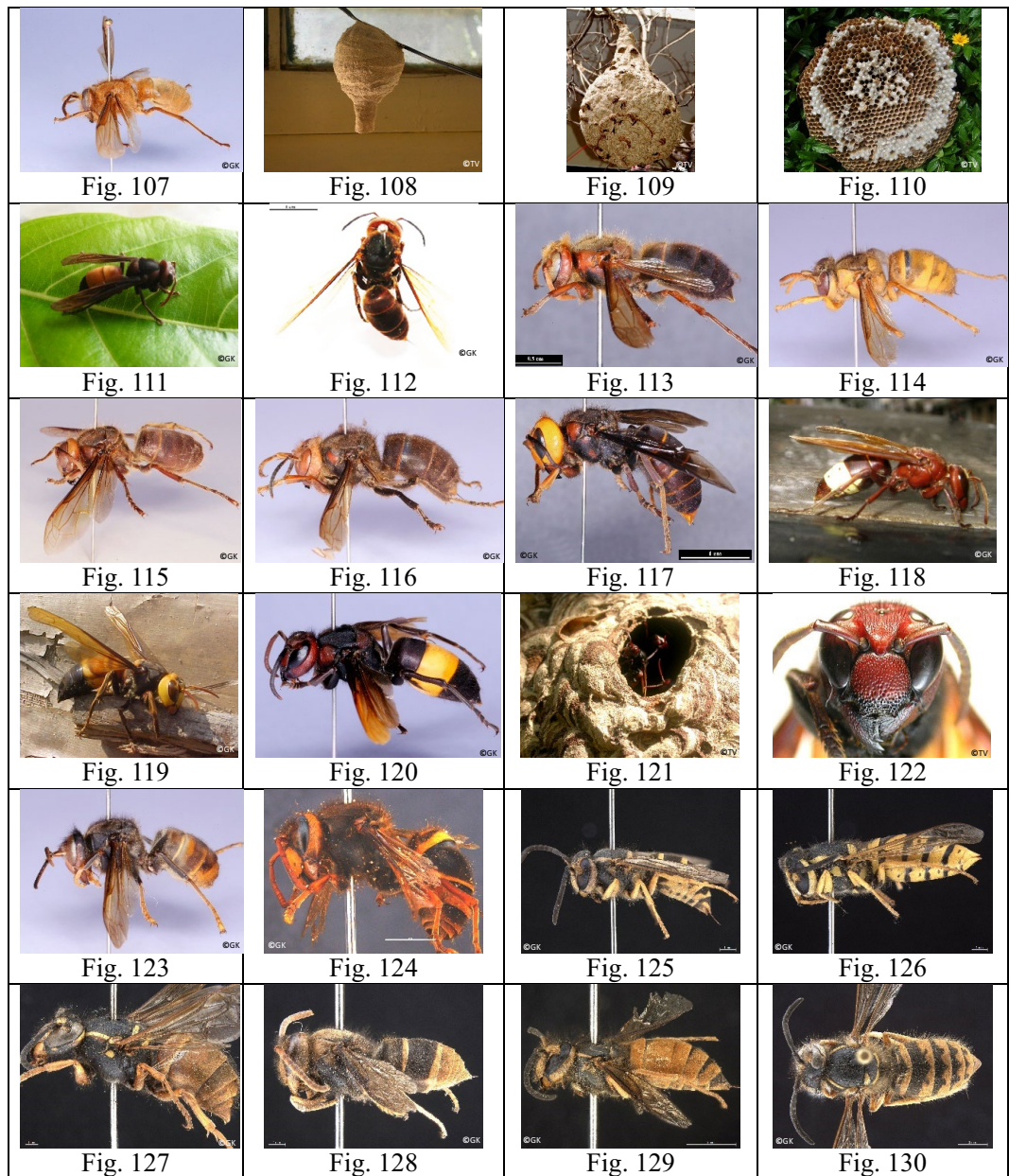


Figure 5: 107. *Provespa barthelemyi*, female. 108 & 109. Nesting sites of the genus *Vespa*. 110. One of the combs from a nest of *V. tropica*. 111. *Vespa affinis*, female. 112. *Vespa analis*, female. 113. *Vespa basalis*, female. 114. *Vespa bicolor*, female. 115. *Vespa binghami*, female. 116. *Vespa fumida*, female. 117. *Vespa mandarinia*, female. 118. *Vespa orientalis*, female. 119. *Vespa soror*, female. 120. *Vespa tropica*, female. 121. *V. tropica* nest showing its single opening. 122. *V. tropica*, head frontal view showing the shape of clypeus. 123. *Vespa velutina*, female. 124. *Vespa vivax*, female. 125. *Vespula flaviceps*, female. 126. *Vespula germanica*, female. 127. *Vespula nursei*, female. 128. *Vespula orbata*, female. 129. *Vespula structor*, female. 130. *Vespula vulgaris*, female.

Nesting habits: The nests of *Vespa bicolor*'s are mostly aerial and found to be in protected locations, such as undersides of roofs, open cavities, in grassland fixed to tall grasses etc. This species also nests in cavities, such as tree hollows or construction cavities¹².

84) *Vespa binghami* du Buysson, 1905 (Fig. 5)

Vespa Binghami du Buysson, 1905 (1904): 488 (key), 523. Lectotype female, Taungoo Hills, Myanmar (PARIS).

Distribution: India: Arunachal Pradesh, Meghalaya, Sikkim, West Bengal; Bhutan; Myanmar. *Elsewhere:* China; Korea; Laos; Russia; Thailand; Vietnam⁶⁴.

85) *Vespa ducalis* Smith, 1852

Vespa ducalis Smith, 1852b: 39. Female, Tieng-tung near Ning-po-foo, China (LONDON).

Distribution: India: Meghalaya, Sikkim; Myanmar; Nepal. *Elsewhere:* China (including Taiwan); Japan; Korea; Russia; Thailand; Vietnam⁶⁴.

Nesting habits: *Vespa ducalis* is known as a fossorial species, nesting in cavities¹². This study observed that its nests do not have a complete envelope.

86) *Vespa dybowskii* André, 1884

Vespa dybowskii André, 1884: 582. Holotype female, Russia: 'Sibérie' (?PARIS).

Distribution: Myanmar. *Elsewhere:* China; Japan; Korea; Russia¹⁴².

87) *Vespa fumida* van der Vecht, 1905 (Fig. 5)

Vespa variabilis du Buysson, 1905 (1904): 490 (key), 522, 627. Lectotype female, Mou-pin, China (PARIS).

Vespa variabilis fumida van der Vecht, 1959b: 228. Padong, Bhutan (PARIS).

Distribution: India: Arunachal Pradesh, Assam, Sikkim, West Bengal; Bhutan; Myanmar; Nepal. *Elsewhere:* China⁶⁴.

88) *Vespa mandarinia* Smith, 1852 (Fig. 5)

Vespa mandarinia Smith, 1852b: 38. Female, "Tein-tung, near Ning-po-foo, amongst the mountains", China (LONDON).

Distribution: India: Arunachal Pradesh, Assam, Himachal Pradesh, Manipur, Meghalaya, Mizoram, Sikkim, Uttarakhand, West Bengal; Bhutan; Myanmar; Nepal; Pakistan; Sri Lanka. *Elsewhere:* China (including Taiwan); Japan; Korea; Laos; Malaysia; Russia; Thailand, Vietnam⁶⁴.

Nesting habits: This species is known to nest underground or in pre-existing cavities¹⁴⁷.

89) *Vespa mocsaryana* du Buysson, 1905

Vespa mocsaryana du Buysson, 1905 (1904): 490 (key), 537. Male, Thagata, Tenasserim (GENOVA).

Distribution: India: Assam, Meghalaya, Sikkim; Myanmar. *Elsewhere:* China (including Hong Kong); Indonesia; Laos; Malaysia; Singapore; Thailand; Vietnam⁶⁴.

90) *Vespa orientalis* Linnaeus, 1771 (Fig. 5)

Vespa orientalis Linnaeus, 1771: 540. Holotype female, "Oriente" (PICCADILLY).

Distribution: India: Andhra Pradesh, Bihar, Delhi, Haryana, Jammu & Kashmir, Jharkhand, Madhya Pradesh, Maharashtra, Odisha, Punjab, Rajasthan, Uttarakhand, Uttar Pradesh, West Bengal; Nepal; Pakistan. *Elsewhere:* Afghanistan; Albania; Algeria; Bahrain; Bosnia & Herzegovina; Bulgaria; China; Croatia; Cyprus; Egypt; Ethiopia; Georgia; Greece; Iran; Iraq; Israel; Italy; Jordan; Kazakhstan; Kyrgyzstan; Lebanon; Libya; Macedonia; Malta; Montenegro; Oman; Romania; Russia; Saudi Arabia; Somalia; Syria; Tajikistan; Turkey; Turkmenistan; U.A.E.; Uzbekistan; Yemen⁶⁴.

91) *Vespa soror* du Buysson, 1905 (Fig. 5)

Vespa ducalis var. *soror* du Buysson, 1905 (1904): 490 (key), 519. Lectotype female, Kiangsi, China (PARIS).

Distribution: India: Arunachal Pradesh, Meghalaya, Nagaland, Uttar Pradesh; Myanmar. *Elsewhere:* China (including Hong Kong); Laos; Thailand; Vietnam⁶⁴.

Nesting habits: This species is known to construct nests in underground cavities dug out from existing hollows with partial envelope¹².

92) *Vespa tropica* (Linnaeus, 1758) (Fig. 5)

Sphex tropica Linnaeus, 1758: 1–517.

Vespa tropica tropica; Bequaert, 1936: 328, key, des., figs.

Distribution: India: Andaman & Nicobar Islands, Andhra Pradesh, Arunachal Pradesh, Assam, Bihar, Chhattisgarh, Goa, Haryana, Himachal Pradesh, Karnataka, Kerala, Madhya Pradesh, Odisha, Puducherry, Sikkim, Tamil Nadu, Telangana, Tripura, Uttarakhand, West Bengal; Bhutan; Myanmar; Nepal; Pakistan; Sri Lanka. *Elsewhere:* Brunei; Cambodia; China; Indonesia; Laos; Malaysia; Philippines; Singapore; Thailand; Vietnam [64; 80].

Nesting habits: The nesting habits are similar to the nesting habits of *V. affinis*. This builds huge, enclosed nests of various sizes with single opening (Fig. 5). Elsewhere it is known to inhabit pre-existing cavities and commonly found affixed to the roof beams of old village houses¹².

Remarks: This species differs from *V. affinis* mainly by its larger size, black markings and by the nature of clypeus (Fig. 5).

93) *Vespa velutina* Lepeletier, 1836 (Fig. 5)

Vespa velutina Lepeletier, 1836: 507. Female, Java, Indonesia (PARIS).

Distribution: India: Arunachal Pradesh, Assam, Himachal Pradesh, Jammu & Kashmir, Meghalaya, Sikkim, Uttarakhand, West Bengal; Bhutan; Myanmar; Pakistan. *Elsewhere:* Afghanistan; China (including Taiwan); Indonesia; Laos; Malaysia; South Korea [introduced]; Thailand; Vietnam⁶⁴.

Nesting habits: This species makes aerial nests on trees and shrubs. He observed that the nests consist of several combs with multilayered envelope¹².

94) *Vespa vivax* Smith, 1870 (Fig. 5)

Vespa vivax Smith, 1870: 190. Female, Binsar, Uttarakhand, India (LONDON).

Distribution: India: Jammu & Kashmir, Himachal Pradesh, Sikkim, Uttarakhand; Bhutan; Myanmar; Nepal. *Elsewhere:* China (including Taiwan); Thailand⁶⁴.

Genus *Vespula* Thomson, 1896

Vespula Thomson, 1869: 79. Type species: *Vespa austriaca* Panzer, 1799.

Pseudovespa Schmiedeknecht, 1881: 314. Type species: *Vespa austriaca* Panzer, 1799.

Paravespula Blüthgen, 1938a (1937): 271. Type species: *Vespa vulgaris* Linnaeus, 1758.

Allovespula Blüthgen, 1943: 149. Type species: *Paravespula rufa* (Linné) [= *Vespa rufa* Linnaeus, 1758].

Rugovespula Archer, 1982: 261, 264. Type species: *Vespa koreensis* Radoszkowski, 1887.

95) *Vespula austriaca* (Panzer, 1799)

Vespa austriaca Panzer, 1799. Male, "Viennae Austr." (destroyed).

Vespula (*Vespula*) *austriaca*; Guiglia, 1972: 102.

Distribution: India: Jammu & Kashmir; Pakistan. *Elsewhere:* Albania; Austria; Belarus; Belgium; Bosnia & Herzegovina; Bulgaria; Canada; China; Croatia; Czech Republic; Denmark; Estonia; Finland; France; Georgia; Germany; Greece; Hungary; Ireland; Italy; Japan; Kazakhstan; Korea; Kyrgyzstan; Latvia; Liechtenstein; Lithuania; Luxembourg; Macedonia; Moldova; Mongolia; Netherlands; Norway; Poland; Romania; Russia; Serbia; Slovakia; Slovenia; Spain; Sweden; Switzerland; Turkey; U.K.; Ukraine⁶⁴.

96) *Vespula flaviceps* (Smith, 1870) (Fig. 5)

Vespa flaviceps Smith, 1870: 174, 191.

Distribution: India: Arunachal Pradesh, Assam, Himachal Pradesh, Jammu & Kashmir, Manipur, Meghalaya, Sikkim, Uttarakhand, West Bengal; Myanmar; Nepal; Pakistan. *Elsewhere:*

China (including Taiwan); Japan; Korea; Laos; Russia; Thailand; Vietnam⁶⁴.

Nesting habits: This species is known to nests in underground cavities¹⁴⁷.

97) *Vespula germanica* (Fabricius, 1793) (Fig. 5)

Vespa germanica Fabricius, 1793: 256.

Vespula (*Paravespula*) *germanica*; Williams, 1983: 194.

Distribution: India: Arunachal Pradesh, Himachal Pradesh, Jammu & Kashmir; Nepal; Pakistan. *Elsewhere:* Afghanistan; Albania; Algeria; Armenia; Argentina [introduced]; Australia [introduced]; Austria; Azerbaijan; Belarus; Belgium; Bosnia & Herzegovina; Bulgaria; Canada; Chile [introduced]; China (including Taiwan); Croatia; Czech Republic; Denmark; Estonia; Finland; France; Georgia; Germany; Greece; Hungary; Iceland [introduced]; Iran; Iraq; Ireland; Israel; Italy; Jordan; Kazakhstan; Korea; Kyrgyzstan; Lebanon; Liechtenstein; Lithuania; Luxembourg; Macedonia; Malta; Mayotte; Moldova; Mongolia; Morocco; Netherlands; New Zealand [introduced]; Norway; Poland; Portugal; Romania; Russia; Scotland; Serbia; Slovakia; Slovenia; South Africa [introduced]; Spain; Sweden; Switzerland; Syria; Tajikistan; Tunisia; Turkey; Turkmenistan; U.K.; Ukraine; U.S.A. [introduced]; Uzbekistan⁶⁶.

98) *Vespula kingdonwardi* Archer, 1981

Vespula kingdonwardi Archer, 1981b: 54,57 (key), 60, figs. 4C–D. Female, male, [China] "TIBET, 28.25 N 97.55 E" (holotype female LONDON); also from other localities in Xizang; Myanmar.

Distribution: Myanmar; Nepal. *Elsewhere:* China³⁸.

99) *Vespula koreensis* (Radoszkowski, 1887)

Vespa koreensis Radoszkowski, 1887: 432. Lectotype female, "Koree" (LONDON).

Vespula koreensis salebrosa Archer, 1982: 261, 267.

Distribution: India: Meghalaya, Sikkim; Myanmar. *Elsewhere:* China; Korea; Laos; Russia; Thailand; Vietnam⁶⁴.

100) *Vespula nursei* Archer, 1981 (Fig. 5)

Vespula nursei Archer, 1981b: 54, 57. Holotype female, Kashmir, India (LONDON).

Distribution: India: Delhi, Himachal Pradesh, Jammu & Kashmir, Punjab, Sikkim, Uttarakhand; Bhutan; Pakistan. *Elsewhere:* China; Philippines⁶⁴.

101) *Vespa orbata* (du Buysson, 1902)
(Fig. 5)

Vespa orbata du Buysson, 1902: 140. Lectotype female, Darjeeling, West Bengal, India (PARIS).

Distribution: India: Arunachal Pradesh, Nagaland, Sikkim, Uttarakhand, West Bengal; Myanmar; Nepal. *Elsewhere:* China; Laos; Thailand; Vietnam⁶⁴.

102) *Vespa rufa* (Linnaeus, 1758)

Vespa rufa Linnaeus, 1758: 572. "in Europa" (lectotype female, PICCADILLY).

Vespa rufa grahami Archer, 1981b: 54, 62. Female, male, "CHINA, Szechuen, 30 miles north of Tatsienku" (WASHINGTON); also from elsewhere in Sichuan.

Distribution: Nepal. *Elsewhere:* Albania; Austria; Belgium; Bulgaria; Canada; China; Denmark; Croatia; Czech Republic; Finland; France; Georgia; Germany; Ireland; Italy; Japan; Korea; Luxembourg; Mongolia; Netherlands; Norway; Poland; Russia; Spain; Sweden; Switzerland; Taiwan; Turkey; U.K.; Ukraine; U.S.A.; Uzbekistan³⁸.

103) *Vespa structor* (Smith, 1870) (Fig. 5)

Vespa structor Smith, 1870: 191. Female, Binsar, Uttarakhand, India (LONDON).

Distribution: India: Arunachal Pradesh, Assam, Jammu & Kashmir, Himachal Pradesh, Sikkim, Uttarakhand, West Bengal; Myanmar; Nepal. *Elsewhere:* China; Laos; Thailand⁶⁴.

104) *Vespa vulgaris* (Linnaeus, 1758)
(Fig. 5)

Vespa vulgaris Linnaeus, 1758: 572. Lectotype female, "in Europa" (PICCADILLY).

Vespa vulgaris vetus Eck, 1999: 309, 329.

Distribution: India: Himachal Pradesh, Jammu & Kashmir; Pakistan. *Elsewhere:* Albania; Argentina [introduced]; Australia [introduced]; Austria; Azerbaijan; Belarus; Belgium; Bosnia & Herzegovina; Bulgaria; Chile [introduced]; China; Croatia; Czech Republic; Denmark; Estonia; Finland; France; Georgia; Germany; Greece; Hungary; Iceland; Iran; Ireland [introduced]; Israel; Italy; Japan; Kazakhstan; Korea; Kyrgyzstan; Latvia; Liechtenstein; Lithuania; Luxemburg, Macedonia; Mexico; Moldova; Mongolia; Netherlands; New Zealand; Norway; Poland; Portugal; Romania; Russia; Serbia; Slovakia; Slovenia; South Africa; Spain; Sweden; Switzerland; Syria; Tahiti [introduced]; Turkey; U.K.; Ukraine⁶⁴.

4 Discussion

This study includes all species of social Vespidae on the Indian subcontinent. The genus *Polistes* is the largest genus with 42 species followed by *Ropalidia* with 27 species. In comparison to these two genera, other genera are less diverse on the Indian Subcontinent. The genus *Polistes* is the most diverse social wasp with extensive distribution records as well. The genus *Ropalidia* is the second most diverse social wasp, which spreads across whole of the Indian Subcontinent. The recent review by Gawas et al⁶⁴ summarised the current taxonomy of Vespidae of India with their distribution records. Undoubtedly, more studies of the museum samples and field collections will add more species to the list. Dedicated surveys to explore the ecology and biology of these social wasps are in dire need to understand more of their ecology, biology and distribution patterns in the Indian subcontinent.

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Author Contributions

TV contributed the introduction, analysis of the results, ecology, biology and their relevant images. GK contributed the research methodology, taxonomy and distribution part of the results, the corresponding references, and their relevant images.

Both the authors have contributed to the preparation and review of the manuscript.

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