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Monogenea of fishes from the lagoon flats of Palmyra Atoll in the Central Pacific

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Abstract

A survey of the monogeneans of fishes from the lagoon flats of Palmyra Atoll detected 16 species already reported from the Indo-West Pacific faunal region. A total of 653 individual fish from 44 species were collected from the sand flats bordering the lagoon of the atoll. Eighteen species of fish were infected with monogeneans. The monogenean species recovered were: *Benedenia hawaiiensis* on *Acanthurus xanthopterus*, *Chaetodon auriga*, *Chaetodon lunula*, *Mulloidichthys flavolineatus*, *Pseudobalistes flavimarginatus* and *Rhinecanthus aculeatus*; *Ancyrocephalus ornatus* on *Arothron hispidus*; *Euryhaliotrema annulocirrus* on *Chaetodon auriga* and *Chaetodon lunula*; *Euryhaliotrema chrysotaeniae* on *Lutjanus fulvus*; *Euryhaliotrema grandis* on *Chaetodon auriga* and *Chaetodon lunula*; *Haliotrema acanthuri* on *Acanthurus triostegus*; *Haliotrema aurigae* on *Chaetodon auriga* and *Chaetodon lunula*; *Haliotrema dempsteri* on *Acanthurus xanthopterus*; *Haliotrema minutospirale* on *Mulloidichthys flavolineatus*; *Haliotrematoides patellacirrus* on *Lutjanus monostigma*; *Neohaliotrema bombini* on *Abudefduf septemfasciatus* and *Abudefduf sordidus*; *Acleotrema girellae* and *Acleotrema parastromatei* on *Kyphosus cinerascens*; *Cemocotylella elongata* on *Caranx ignobilis*, *Caranx melampygus* and *Caranx papuensis*; *Metamicrocotyla macracantha* on *Crenimugil crenilabris*; and *Pseudopterinotrema albulae* on *Albula glossodonta*. All these monogenean–host combinations represent new geographical records. The monogenean species composition of the Palmyra Atoll is similar to that of the Hawaiian Islands. However, the number of species recovered was lower compared with other localities within the Indo-West Pacific, perhaps due to the geographical isolation of Palmyra Atoll.

Keywords

Monogenea, fish, geographical isolation, islands, Indo-Pacific, atoll

Introduction

Several studies on the parasitic fauna of marine fishes have been conducted at different localities in the Indo-West Pacific, including off the Great Barrier Reef (Australia), New Caledonia, Moorea (French Polynesia), Malaysia, South China, and the Hawaiian Islands (Yamaguti 1965, 1968, Young 1968, Plaisance et al. 2004, Plaisance and Kritsky 2004, Lim and Justine 2007, Kritsky et al. 2009, Lim and Gibson 2008, 2009, 2010, Rehulkova et al. 2010, Palm and Bray 2014, Mendoza-Franco et al. 2017).

Palmyra Atoll is one of the northern Line Islands located in the East Indo-Pacific marine ecoregion (Spalding et al. 2007), 1680 km south-south-west of Hawaii. It is presently a marine protected area and lacks regular human settlement since World War II. The Palmyra Atoll represents a relatively long history with little to no exploitation (Lafferty et al. 2008). All fishing has been prohibited at Palmyra since it became a US National Wildlife Refuge in 2000 (before that, its remoteness kept fishing pressure low). As a part of a larger research project on the role of infectious agents in the Palmyra Atoll ecosystem, we had the opportunity to undertake a survey of the fish parasites from the lagoon flats of this coral atoll. The goals of the present paper were to report the monogenean species recovered and to establish their zoogeographical affinities with respect to the Indo-West Pacific (IWP) ecoregion.

Methods

Between 13 October and 10 November 2009, and 22 June and 28 July 2010, we captured fishes by seine, spear, and hook and line from the intertidal sand flats bordering the lagoon of Palmyra Atoll (5°53'00"N; 162°05'00"W), U.S.A. Immediately after capture, the fish were separated and anesthetised individually with 0.5 ml L^{-1} of 2-phenoxyethanol (Sigma, St. Louis, MO, USA) in plastic bags with lagoon water to avoid loss or mixing of monogeneans among fishes and transported them to the laboratory facility of the Palmyra Atoll Research Consortium (PARC). We examined only freshly killed fish (and the bag water). Observations were under a stereomicroscope with a total magnification of 40×. For each individual host, the skin was examined and the gill arches removed, examined, and the monogeneans obtained were counted, preliminarily identified, and most of them (70–80%) fixed in 4% hot formalin, labelled, and stored in vials for later evaluation. The remaining specimens were flattened and mounted in glycerine ammonium picrate mixture (GAP) to study the morphology of sclerotized structures under a compound microscope (Olympus BX-53, Olympus Corporation, Tokyo, Japan). After evaluation, the specimens that had been fixed with GAP were remounted in Canada balsam (Ergens 1969). Unflattened specimens were cleared with Gray & Wess medium or stained in trichrome and mounted in Canada balsam (for details of these techniques, see Vidal-Martínez et al. 2001). In this manuscript, the male copulatory organ of the monogeneans is denoted below as the MCO. Prevalence and mean intensity concepts were applied following Bush et al. (1997). Specimen of each species were deposited in the United States National Parasite Collection, NMNH Invertebrate Zoology, Smithsonian Museum Support Center, MD, USA (USNM), and the Helminthological Collection of the Laboratory of Parasitology, at Centre for Research and Advanced Studies, National Polytechnic Institute, Mérida, Yucatán, México (CHCM).

Results

Monogeneans of fishes from the Palmyra lagoon flats

During this study, 653 individual fish belonging to 44 species were collected (Table 1). The 16 species of monogeneans infected 18 fish species (Table 2). Those hosts with the most monogenean species were *Chaetodon auriga* Forsskål and *Chaetodon lunula* (Lacépède) with four species, and *Kyphosus cinerascens* (Forsskål), *Acanthurus xanthopterus* Valenciennes and *Mulloidichthys flavolineatus* (Lacépède) with two species each. All other fish species harboured one monogenean species. Twenty-six additional fish species were examined, but no monogeneans were found (Table 2).

Monogenea van Beneden, 1858
Monopisthocotylea Odhner, 1912
Capsalidae Baird, 1853

Benedenia hawaiiensis Yamaguti, 1968

Type host. *Priacanthus cruentatus* (Lacépède) (Priacanthidae)

Other host and localities. *Benedenia hawaiiensis* has been reported from more than 24 species of fishes from off Hawai'i (Whittington et al. 2001). From *Sargocentron spiniferum* (Forsskål) (Holocentridae) in the South China Sea (as *Benedenia sargocentron*) (Zhang et al. 2001).

Current host. *Acanthurus xanthopterus* (Acanthuridae), *Chaetodon auriga*, *Chaetodon lunula* (Chaetodontidae), *Mulloidichthys flavolineatus* (Lacépède) (Mullidae), *Pseudobalistes flavimarginatus* (Rüppell) and *Rhinecanthus aculeatus* (Linnaeus) (Balistidae).

Site infection. Gills.

Prevalence and mean intensity. *Acanthurus xanthopterus* 5 and 2 (n = 20); *Chaetodon auriga* 7,7 and 1 (n = 13); *Chaetodon lunula* 14,3 and 1±0 (n = 14); *Mulloidichthys flavolineatus* 7,7 and 2±0,6 (n = 52); *Pseudobalistes flavimarginatus* 25 and 1 (n = 4) and *Rhinecanthus aculeatus* 16,7 and 3±2 (n = 18).

Specimens deposited. CHCM No. 551 (paratypes) (1 slide, 1 specimen).

Remarks. *Benedenia hawaiiensis* was originally described by Yamaguti (1968) from the gills and fins of *Priacanthus cruentatus* off Hawai'i. Zhang et al. (2001) described *Benedenia sargocentron* on *Sargocentron spiniferum* from the South China Sea. However, Deveney and Whittington (2010) determined that *B. sargocentron* was a junior synonym of *B. hawaiiensis*, and proposed keeping *B. hawaiiensis* as the valid name. *Benedenia hawaiiensis* is characterized by having an opisthaptor which is usually a little longer than wide, provided with a marginal membrane and is notched opposite the marginal hooklets; with 14 marginal hooklets; two between the posterior anchors. The marginal valve is clearly indented at each hooklet and also at the position where the posterior anchor meets the haptor edge. The marginal valve is conspicuous and has one lobe between each of the hooklets around the circumference of the haptor with the anterior lobes being larger and wider. The proximal ends of the anterior anchors overlap the proximal ends of the accessory sclerites, and the distal portion of the anterior anchors overlap the posterior anchors for two-thirds of their lengths. The accessory sclerites are alate and raise the ventral haptoral tissues through which they protrude. The MCO is muscular, well-equipped with circular and longitudinal muscle fibres and lies in a cavity or canal with poorly developed muscle walls. The most prominent feature of the MCO of *B. hawaiiensis* is that it tapers to form a narrow distal tip. The presence of *B. hawaiiensis* on the gills of *R. aculeatus* at Palmyra Atoll represents both a new host and a new geographical record for this species.

Dactylogyridae Bychowsky, 1933

Ancyrocephalus ornatus Yamaguti, 1968

Type host. *Arothron hispidus* (Linnaeus) (Tetraodontidae).

Other host and localities. *Arothron hispidus*, Hawai'i (Yamaguti 1968).

Current host. *Arothron hispidus.*

Site infection. Gills.

Prevalence and mean intensity. 93,3 and 47 ± 69 (n=15).

Specimens deposited. CHCM No. 550 (paratypes) (1 slide, 1 specimen), USNM No. 1459841 (voucher) (1 slide, 1 specimen).

Remarks. Originally described by Yamaguti (1968) from gills of *A. hispidus* off Hawai'i, this species has recently been reported by Palm and Bray (2014) from the same host and locality. It is characterized by the cirrus being ornamented distally with a spiral fold, hence the specific name. New geographical record for Palmyra Atoll.

Euryhaliotrema annulocirrus (Yamaguti, 1968) Kritsky, 2012

Type host. *Chaetodon auriga* (Chaetodontidae).

Other host and localities. *Chaetodon auriga*, Hawai'i (Yamaguti 1968; Mizelle and Kritsky 1969), *Chaetodon lunula*, Hawai'i (Yamaguti 1968; Mizelle and Kritsky 1969), *Chaetodon bellamaris* (= *C. wiebeli*) Kaup from the South China Sea (Zhang et al. 2003), *Chaetodon modestus* Temminck and Schlegel from the South China Sea (Zhang et al. 2003), *Roa modesta* and *Chaetodon vagabundus* Linnaeus from Moorea, French Polynesia, Great Barrier Reef, Australia, Palau, New Caledonia (all Chaetodontidae).

Current host. *Chaetodon auriga* and *Chaetodon lunula* (Chaetodontidae).

Site infection. Gills.

Prevalence and mean intensity. 53,8 and 22±22 (n=13) to *C. auriga*; 71,4 and 42±18 (n=14) to *C. lunula.*

Specimens deposited. CHCM No. 542 (paratypes) (1 slide, 1 specimen) (for *C. auriga*), CHCM No. 543 (paratypes) (1 slide, 2 specimen) (for *C. lunula*), USNM No. 1459842 (voucher) (1 slide, 1 specimen) (for *C. lunula*).

Remarks. This species was originally described by Yamaguti (1968) as *Haliotrema annulocirrus* and transferred to the genus *Euryhaliotrematoides,* as *E. annulocirrus,* by Plaisance and Kritsky (2004). Recently, Kritsky (2012) proposed the synonymy of *Euryhaliotrematoides* with *Euryhaliotrema*. As result, this species was transferred as *Euryhaliotrema annulocirrus*. *Haliotrema annulocirrus* Yamaguti 1968, *Euryhaliotrematoides annulocirrus* (Yamaguti 1968) Plaisance and Kritsky 2004, *Parahaliotrema affinis* Mizelle and Kritsky 1969, *Haliotrema affinis* (Mizelle and Kritsky 1969) Vala et al. 1982 and *Haliotrema angulocirrus* Yamaguti 1968 are considered synonyms of this species. *Euryhaliotrema annulocirrus* is distinguished from all other species of the genus by having an enlarged slit-like vaginal pore with serrated posterior lip and a conspicuous, elongate and heavy coiled tube of the MCO. New geographical record for Palmyra Atoll.

Euryhaliotrema chrysotaeniae (Young, 1968) Kritsky & Boeger, 2002

Type host. *Lutjanus chrysotaenia* (=*L. carponotatus*) (Richardson) (Lutjanidae).

Other host and localities. Gills of *L. chrysotaenia* (=*L. carponotatus*) from Heron Island, Queensland, Australia (as *Haliotrema chrysotaeniae*) (Young 1968). *Lutjanus fulvus* (Forster), *Lutjanus fulviflamma* (Forsskål), *Lutjanus quinquelineatus* (Bloch) and *Lutjanus russellii* (Bleeker) from Nouméa, New Caledonia (Kritsky 2012). *Lutjanus fulvus* and *Lutjanus kasmira* (Forsskål) from French Polynesia and Hawaiian Islands (all as *Euryhaliotrema chrysotaeniae*) (Vignon et al. 2009). *Lutjanus russellii* from Guangdong Province, China (as *Euryhaliotrema chrysotaeniae*) (Li and Yan 2007) (all Lutjanidae).

Current host. *Lutjanus fulvus* (Lutjanidae).

Site infection. Gills.

Prevalence and mean intensity. 50 and 15 ± 25 (n=26).

Specimens deposited. CHCM No. 537 (paratypes) (1 slide, 1 specimen).

Remarks. Originally described by Young (1968) as *Haliotrema chrysotaeniae* and transferred to the genus *Euryhaliotrema* by Kritsky and Boeger (2002) as *E. chrysotaeniae*. *Euryhaliotrema chrysotaeniae* has a delicate MCO with more than three rings and an elongate meandering vaginal canal. New geographical record for Palmyra Atoll.

Table 1. Fish species examined from the lagoon flats of Palmyra Atoll. N = number of fish examined; Max = maximum length reported for that fish species in FishBase (http://www.fishbase.se); Range = total length range of the fish examined.

Host examined	Fish common name	N	Infected hosts	Max (cm)	Range (cm)
Acanthuridae					
Acanthurus triostegus (Linnaeus, 1758)	Convict surgeon	50	22	27	10–18
Acanthurus xanthopterus Valenciennes, 1835	Yellowfin surgeon	20	16	70	20–40
Albulidae					
Albula glossodonta (Forsskål, 1775)	Roundjaw bonefish	24	17	90	37–58
Apogonidae					
Cheilodipterus quinquelineatus Cuvier, 1828	Five-lined cardinalfish	5	0	13	5–6
Balistidae					
Pseudobalistes flavimarginatus (Rüppell, 1829)	Yellowmargin triggerfish	4	1	60	17–53
Rhinecanthus aculeatus (Linnaeus, 1758)	Blackbar triggerfish	18	3	30	8–24
Belonidae					
Platybelone argalus (Lesueur, 1821)	Keeltail needlefish	2	0	50	9–36
Carangidae					
Carangoides ferdau (Forsskål, 1775)	Blue trevally	5	0	75	33 – 38
Carangoides orthogrammus (Jordan & Gilbert, 1882)	Island trevally	3	0	75	25 – 35
Caranx ignobilis (Forsskål, 1775)	Giant trevally	4	2	170	56–79
Caranx melampygus Cuvier, 1833	Bluefin trevally	6	1	117	31–66
Caranx papuensis Alleyne & MacLeay, 1877	Brassy trevally	5	2	88	12–41
Carcharhinidae					
Carcharhinus melanopterus (Quoy & Gaimard, 1824)	Blacktip reef shark	5	0	200	46–219
Chaetodontidae					
Chaetodon auriga Forsskål, 1775	Threadfin butterflyfish	13	9	23	12–19
Chaetodon lunula (Lacépède, 1802)	Raccoon butterflyfish	14	11	20	11–16
Chanidae					
Chanos chanos (Forsskål, 1775)	Milkfish	5	0	180	31–57
Gobiidae					
Amblygobius phalaena (Valenciennes, 1837)	Whitebarred goby	18	0	15	1.3–7
Asterropteryx semipunctata Rüppell, 1830	Starry goby	12	0	6	2–4
Gnatholepis anjerensis (Bleeker, 1851)	Eye-bar goby	2	0	8	2–3
Istigobius decoratus (Herre, 1927)	Decorated goby	5	0	13	7–11
Istigobius ornatus (Rüppell, 1830)	Ornate goby	26	0	11	3–6
Istigobius rigilius (Herre, 1953)	Rigilius goby	1	0	11	4
Oplopomus oplopomus (Valenciennes, 1837)	Spinecheek goby	26	0	10	2–7
Psilogobius prolatus Watson & Lachner, 1985	Longjaw shrimpgoby	11	0	6	2–4
Valenciennea sexguttata (Valenciennes, 1837)	Sixspot goby	14	0	14	2–9
Hemiramphidae					
Hemiramphus depauperatus Lay & Bennett, 1839	Tropical half-beak fish	20	0	40	20–34
Kyphosidae					
Kyphosus cinerascens (Forsskål, 1775)	Blue sea chub	2	2	50	35–38
Lutjanidae					
Lutjanus fulvus (Forster, 1801)	Blacktail snapper	26	13	40	7–26
Lutjanus monostigma (Cuvier, 1828)	One spot snapper	6	2	60	17–37

Host examined	Fish common name	N	Infected hosts	Max (cm)	Range (cm)
Mugilidae					
Crenimugil crenilabis (Forsskål, 1775)	Fringelip mullet	42	2	60	8–45
Liza vaigiensis (Quoy & Gaimard, 1825)	Squaretail mullet	54	0	63	3–32
Valamugil engeli (Bleeker, 1858)	Kanda	63	0	30	1–20
Mullidae					
Mulloidichthys flavolineatus (Lacépède, 1801)	Yellowstripe goatfish	52	10	43	8–37
Upeneus taeniopterus Cuvier, 1829	Finstripe goatfish	5	0	33	1–30
Muraenidae					
Gymnothorax pictus (Ahl, 1789)	Paintspotted moray	7	0	140	41–70
Ophichthidae					
Myrichthys colubrinus (Boddaert, 1781)	Harlequin snake eel	3	0	97	33–65
Pinguipedidae					
Parapercis lata Randall & McCosker, 2002	Y-Barred Sandperch	13	0	21	2–3
Pomacentridae					
Abudefduf septemfasciatus (Cuvier, 1830)	Banded sergeant	12	3	23	14–20
Abudefduf sordidus (Forsskål, 1775)	Blackspot sergeant	18	5	24	14–19
Chrysiptera glauca (Cuvier, 1830)	Grey demoiselle	3	0	12	8–10
Stegastes nigricans (Lacépède, 1802)	Dusky farmerfish	10	0	14	8–10
Serranidae					
Epinephelus merra Bloch, 1793	Honeycomb grouper	2	0	32	13–24
Sphyraenidae					
Sphyraena barracuda (Edwards, 1771)	Great barracuda	2	0	200	65–76
Tetraodontidae					
Arothron hispidus (Linnaeus, 1758)	White–spotted puffer	15	14	50	17–49

Table 2. Monogeneans of fishes from the lagoon flats of Palmyra Atoll; N = number of fish examined.

	Hosts	N	Infected hosts	Prevalence (%)	Mean intensity (± SD)
Capsalidae					
Benedenia hawaiiensis	*Acanthurus xanthopterus*	20	1	5	2
	Chaetodon auriga	13	1	7,7	1
	Chaetodon lunula	14	2	14,3	1 ± 0
	Mulloidichthys flavolineatus	52	4	7,7	2 ± 0,6
	Pseudobalistes flavimarginatus	4	1	25	1
	Rhinecanthus aculeatus	18	3	16,7	3 ± 2
Dactylogyridae					
Ancyrocephalus ornatus	*Arothron hispidus*	15	14	93,3	47 ± 69
Euryhaliotrema annulocirrus	*Chaetodon auriga*	13	7	53,8	22 ± 22
	Chaetodon lunula	14	10	71,4	42 ± 18
Euryhaliotrema chrysotaeniae	*Lutjanus fulvus*	26	13	50	15 ± 22
Euryhaliotrema grandis	*Chaetodon auriga*	13	4	30,8	17 ± 19
	Chaetodon lunula	14	5	35,7	28 ± 19
Haliotrema acanthuri	*Acanthurus triostegus*	50	22	44	13 ± 17
Haliotrema aurigae	*Chaetodon auriga*	13	4	30,8	61 ± 49
	Chaetodon lunula	14	5	35,7	66 ± 20

	Hosts	N	Infected hosts	Prevalence (%)	Mean intensity (± SD)
Haliotrema dempsteri	*Acanthurus xanthopterus*	20	16	80	35 ± 28
Haliotrema minutospirale	*Mulloidichthys flavolineatus*	52	10	19,2	27 ± 18
Haliotrematoides patellacirrus	*Lutjanus monostigma*	6	2	33,3	145 ± 197
Neohaliotrema bombini	*Abudefduf septemfasciatus*	12	3	25	4 ± 2
	Abudefduf sordidus	18	5	27,8	138 ± 97
Diplectanidae					
Acleotrema girellae	*Kyphosus cinerascens*	2	2	100	84 ± 90
Acleotrema parastromatei	*Kyphosus cinerascens*	2	1	50	50
Heteraxinidae					
Cemocotyllela elongata	*Caranx ignobilis*	4	2	50	7 ± 7
	Caranx melampygus	6	1	16,7	4
	Caranx papuensis	5	2	40	7 ± 7
Microcotylidae					
Metamicrocotyla macracantha	*Crenimugil crenilabis*	42	2	4,8	3 ± 1
Pterinotrematidae					
Pseudopterinotrema albulae	*Albula glossodonta*	24	17	70,8	17 ± 18

Euryhaliotrema grandis (Mizelle & Kritsky, 1969) Kritsky, 2012

Type host. *Chaetodon auriga* (Chaetodontidae)

Other host and localities. Gills of several species of Chaetodontidae. *Chaetodon auriga* and *C. lunula* in Hawai'i (as *Parahaliotrema grandis*) (Mizelle and Kritsky 1969); *Chaetodon chrysurus* (=*C. paucifasciatus*) Ahl in the Red Sea (as *Haliotrema grandis*) (Paperna 1972). Plaisance and Kritsky (2004) recorded *E. grandis* on gills of *Chaetodon auriga* and *Chaetodon citrinellus* Cuvier from the coral reefs of Micronesia, French Polynesia, Wallis, Australia and New Caledonia; *Chaetodon ephippium* Cuvier from Wallis and Lizard Island, Australia; *Chaetodon kleinii* Bloch from off Wallis, Australia and Micronesia; *Chaetodon lineolatus* Cuvier from off Heron Island, Australia; *C. lunula* from off French Polynesia, Wallis and Micronesia; *Chaetodon ornatissimus* Cuvier from French Polynesia and Wallis; *Chaetodon trifasciatus* Park from Wallis; *C. vagabundus* from the coral reefs of Micronesia, French Polynesia, Wallis, Australia and New Caledonia; and *Heniochus chrysostomus* Cuvier from off Moorea, French Polynesia. Only one chaetodontid host was found parasitised at Palmyra Atoll.

Current host. *Chaetodon auriga* and *Chaetodon lunula.*

Site infection. Gills.

Prevalence and mean intensity. *Chaetodon auriga* 30.8 and 17±19 (n = 13).
and *Chaetodon lunula* 35.7 and 28±19 (n = 14).

Specimens deposited. CHCM No. 544 (paratypes) (1 slide, 1 specimen), USNM No. 1459843 (voucher) (1 slide, 2 specimen).

Remarks. *Euryhaliotrema grandis* was described by Mizelle and Kritsky (1969) as *Parahaliotrema grandis* and subsequently transferred to *Haliotrema* by Paperna (1972) as *Haliotrema grandis*. Plaisance and Kritsky (2004) erected the genus *Euryhaliotrematoides* and transferred several species of *Haliotrema* to this genus, including *Euryhaliotrematoides grandis*. Recently, Kritsky (2012) proposed the synonymy of *Euryhaliotrematoides* with *Euryhaliotrema*. As a consequence, *Euryhaliotrematoides grandis* was transferred to *Euryhaliotrema* as *Euryhaliotrema grandis*. *Euryhaliotrema grandis* presents a delicate MCO, comprising approximately two rings. Accessory piece variable, serving as a guide for the distal portion of the MCO and is articulated to the base of MCO. Anchors lacking hinged bases. Ventral anchor with flattened base supporting a short deep root, moderately long superficial root, short shaft and point extending to the level of the tip of the superficial root. Dorsal anchor with a short deep root, elongate superficial root, broad base, short shaft, point extending to the level of the superficial root. Ventral bar V-shaped, with an anteromedial concavity having a straight anterior margin and a posterior rounded expansion. Dorsal bar, rod shaped, straight. New geographical record for Palmyra Atoll.

Haliotrema acanthuri Yamaguti, 1968

Type host. *Acanthurus sandvicensis* (=*A. triostegus*) (Linnaeus) (Acanthuridae).

Other host and localities. Yamaguti (1968) recorded *Haliotrema acanthuri* from *Acanthurus sandvicensis* (=*A. triostegus*) in Hawai'i. It has also been found by Palm and Bray (2014) on *A. triostegus* also in Hawai'i (all Acanthuridae).

Current host. *Acanthurus triostegus* (Acanthuridae).

Site infection. Gills.

Prevalence and mean intensity. 44 and 13± 17 (n=50).

Specimens deposited. CHCM No. 548 (paratypes) (1 slide, 1 specimen), USNM No. 1459844 (voucher) (1 slide, 1 specimen).

Remarks. This species is characterized by the morphology of its copulatory complex, which has a bell-shaped base and a short cylindrical shaft, from which arises a proper MCO, and a similar, solid, shorter spike projecting from the genital pore. New geographical record for Palmyra Atoll.

Haliotrema aurigae (Yamaguti, 1968) Plaisance, Bouamer & Morand, 2004

Type host. *Chaetodon auriga* (Chaetodotidae).

Other host and localities. *Chaetodon auriga* from Hawai'i (Yamaguti 1968). On *C. auriga*, *C. citrinellus*, *C. vagabundus*, *C. ephippium*, *C. lunulatus*, *C. kleinii*, *C. lunula*, *C. ornatissimus*, *C. reticulatus*, *C. trifascialis* and *H. chrysostomus* from several sites of the Indo-West Pacific Ocean (Palau Micronesia, Moorea French Polynesia, Wallis and Futuna, New Caledonia, Heron Island and Lizard Island, Australia) (Plaisance et al. 2004).

Recently, this species was reported on *C. auriga* from off the Pratas Islands, South China Sea (Kritsky et al. 2009) and Hawai'i (Palm and Bray 2014) (all Chaetodotidae).

Current host. *Chaetodon auriga* and *Chaetodon lunula* (Chaetodotidae).

Site infection. Gills.

Prevalence and mean intensity. 30,8 and 61±49 (n=13) to *C. auriga* and 35,7 and 66±20 (n=14) to *C. lunula.*

Specimens deposited: CHCM No. 545 (paratypes) (1 slide, 3 specimens), USNM No. 1459845 (voucher) (1 slide, 6 specimen).

Remarks. This species was described for the first time by Yamaguti (1968) as *Pseudohaliotrematoides aurigae*. In 2004, Plaisance et al. recorded this species from 10 species of *Chaetodon* and one species of *Heniochus* (Chaetodontidae), and transferred it to the genus *Haliotrema* as *H. aurigae*. *Haliotrema aurigae* presents a tubular MCO bent near base base; base trapezoid; filamentous accessory piece, elongated, serving as a guide for the distal portion of the MCO. Dorsal anchor base/shaft junction hinged, with elongate superficial root and short, deep root. Ventral anchor with short roots and broad, slightly fenestrated base. Dorsal bar straight, bone-shaped. Ventral bar rod-shaped, an inverted broad U. New geographical record for Palmyra Atoll.

Haliotrema dempsteri (Mizelle & Price, 1964) Young, 1968

Type host. *Acanthurus xanthopterus.*

Other host and localities. *Acanthurus mata* Cuvier, *Acanthurus dussumieri* Valenciennes and *A. xanthopterus* in Australia (Young 1968). Mizelle and Price (1964) recorded it previously from the gills of the *Zanclus canescens* (=*Z. cornutus*) (Linnaeus) (as *Parahaliotrema dempsteri*).

Current host. *Acanthurus xanthopterus.*

Site infection. Gills.

Prevalence and mean intensity. 80 and 35±28 (n=20).

Specimens deposited. CHCM No. 549 (paratypes) (1 slide, 4 specimen), USNM No. 1459846 (voucher) (1 slide, 1 specimen).

Remarks. *Haliotrema dempsteri* was originally described as *Parahaliotrema dempsteri* by Mizelle and Price (1964). Later, Young (1968) recorded it from *A. mata*, *A. dussumieri* and *A. xanthopterus*, redescribing and transferring it to *Haliotrema*. The most relevant morphological characteristics are: haptor subhexagonal, broader than long; one dorsal and one ventral pair of anchors, similar in size and shape; superficial root of each anchor base longer than the deep root; shafts solid and points without formation of a definite angle; wings low and inconspicuous on dorsal anchor shafts, apparently absent on ventral shafts; copulatory complex composed of an MCO and an elongate accessory piece attached to the proximal portion of the MCO shaft, terminating in a recurved tip; and MCO tubular with relatively large base and an undulate shaft. New geographical record for Palmyra Atoll.

Haliotrema minutospirale Yamaguti, 1968

Type host. *Parupeneus cyclostomus* (Lacépède) (Mullidae).

Other host and localities. Yamaguti (1968) recorded this species from gills of *P. cyclostomus, P. pleurostigma* (Bennett) and *P. multifaciatus* (Quoy and Gaimard) for Hawai'i. Palm and Bray (2014) also recorded this species from *P. cyclostomus* in the same locality (all Mullidae).

Current host. *Mulloidichthys flavolineatus* (Mullidae) (New host).

Site infection. Gills.

Prevalence and mean intensity. 19,2 and 27±18 (n=52).

Specimens deposited. CHCM No. 539 (paratypes) (1 slide, 1 specimen), USNM No. 1459850 (voucher) (1 slide, 1 specimen)

Remarks. The morphology of the copulatory complex is a relevant characteristic for its identification. Its MCO consists of an anterior, spiral, flanged portion and a posterior, cylindrical portion, enclosed in a sheath of circular muscular fibres. The presence of *H. minutospirale* on the gills *Mulloidichthys flavolineatus* from Palmyra Atoll represents both a new host and a new geographical record.

Haliotrematoides patellacirrus (Bychowsky & Nagibina, 1971) Kritsky, Yang & Sun, 2009

Type host. *Lutjanus lutjanus* (Bloch) (Lutjanidae).

Other host and localities. Previous records (as *Haliotrema patellacirrus*) on *L. lutjanus* and *L. fulviflamma* from South China Sea (Bychowsky and Nagibina 1971). Kritsky et al. (2009) recorded this species (as *Haliotrematoides patellacirrus*) on *L. russellii*, *L. fulvus*, *Lutjanus vitta* (Quoy and Gaimard) and *L. quinquelineatus* from off New Caledonia; *L. fulviflamma* from Australia; and *Lutjanus ehrenbergii* (Peters) from Nabq Bay, Ras Mohammed National Park (South Sinai, Red Sea) Egypt (all Lutjanidae).

Current host. *Lutjanus monostigma* (Lutjanidae) (New host).

Site infection. Gills.

Prevalence and mean intensity. 33,3 and 145±197 (n=6).

Specimens deposited. CHCM No. 538 (paratypes) (1 slide, 3 specimen).

Remarks. *Haliotrematoides patellacirrus* presents an MCO comprising a proximal platter-shaped base, distal tubular shaft with aloose clockwise coil of about 3/4 of a ring, enclosed in a sheath with a subterminal knob-like projection. Ventral anchor with elongate superficial root, knob-like deep root, shaft slightly narrowed distally and straight, recurved point with delicate superficial grooves. Dorsal anchors with elongate superficial root, inconspicuous (or absent) deep root, straight shaft of varying diameter and recurved point; distal shaft and point superficially grooved. Ventral bar with two submedial pockets along anterior margin; dorsal bar rod-shaped, with subterminal notches, ending slightly narrower than medial portion of bar. The presence of *H. patellacirrus* from *L. monostigma* off Palmyra Atoll represents both a new host and a new geographical record. Only one host was found parasitised.

Neohaliotrema bombini Lim & Gibson, 2010

Type host. *Abudefduf vaigiensis* (Quoy and Gaimard) (Pomacentridae).

Other host and localities. *Abudefduf vaigiensis* from Pulau Langkawi, Malaysia (Lim and Gibson 2010) (Pomacentridae).

Current host. *Abudefduf septemfasciatus* (Cuvier) (New host) and *Abudefduf sordidus* (Forsskål) (Pomacentridae) (New host).

Site infection. Gills.

Specimens deposited. CHCM No. 546 (paratypes) (1 slide, 1 specimen) (for *A. septemfasciatus*), CHCM No. 547 (paratypes) (1 slide, 1 specimen) (for *A. sordidus*), USNM No. 1459851 (voucher) (1 slide, 1 specimen) (for *A. sordidus*).

Prevalence and mean intensity. 25 and 4±2 (n=12) to *A. septemfasciatus* and 27,8 and 138±97 (n = 18) to *A. sordidus.*

Remarks. This species can be distinguished from other members in the genus by having an inconspicuously sclerotised MCO, consisting of a simple, curved, short tube with a large initial part and simple, bifid stick-like accessory piece. This species also has V-shaped bars with processes, 'marginal' hooks of different sizes, anchors with a spatulate, recurved and grooved point, and a non-fenestrated haptor. The presence of *N. bombini* in *A. septemfasciatus* and *A. sordidus* off Palmyra Atoll represents both new hosts and geographical records for this species.

Diplectanidae Monticelli, 1903

Acleotrema girellae Johnston & Tiegs, 1922

Type host. *Girella tricuspidata* (Quoy and Gaimard) (Kyphosidae).

Other host and localities. *Girella tricuspidata* from off Caloundra, southeast of Queensland, Australia (Johnston and Tiegs 1922). *Kyphosus cinerascens* collected off Hawai'i (as *Acleotrema kyphosi*) (Yamaguti 1968). *Kyphosus elegans* (Peters) from Chamela Bay, Mexico (as *Heteroplectanum kyphosi*) (León-Régagnon et al. 1997). *Kyphosus* spp. (as *A. girellae*) from Australia, the Mediterranean Sea and Mexican Pacific (Domingues and Boeger 2007) (all Kyphosidae).

Current host. *Kyphosus cinerascens* (Kyphosidae).

Site infection. Gills.

Specimens deposited. CHCM No. 540 (paratypes) (1 slide, 2 specimen), USNM No. 1459852 (voucher).

Prevalence and mean intensity. 100 and 84±90 (n=2).

Remarks. *Acleotrema girellae* was originally described from the gills of *G. tricuspidata* collected off Caloundra, southeast Queensland, Australia (Johnston and Tiegs 1922). In 1937, Price transferred this species to *Diplectanum* as *D. girellae,* considering *Acleotrema* a junior synonym of *Diplectanum*, based on the presence of squamodiscs. However, Yamaguti (1963) accepted *Acleotrema* as a valid genus. Rakotofiringa et al. (1987) proposed the genus *Heteroplectanum* and several species have been transferred to this new genus, including *Diplectanum kyphosi* (considered a synonym of *A. girellae*) as *Heteroplectanum kyphosi* (Yamaguti, 1968) Oliver 1987. However, Domingues and Boeger (2007) considered that species of *Acleotrema* share unique features and can be distinguished from other diplectanids (including species of *Diplectanum*), presenting arguments for considering *Heteroplectanum* as a junior synonym of *Acleotrema*. Therefore, *Acleotrema kyphosi* Yamaguti, 1968, *Diplectanum girellae* (Johnston & Tiegs, 1922), *Heteroplectanum kyphosi* (Yamaguti, 1968) Oliver, 1987, *Acleotrema gibsoni* Young, 1970 and *Acleotrema heronensis* Young, 1970, are considered synonyms of *A. girellae*. This species differs from its congeners by having: a tubular MCO with the distal extremity recurved and bifid; and a sclerotised sac with radial musculature involving the proximal portion of the MCO. New geographical record for Palmyra Atoll.

Acleotrema parastromatei (Rakotofiringa, Oliver & Lambert, 1987) Domingues & Boeger, 2007

Type host. *Parastromateus niger* (Bloch) (Carangidae).

Other host and localities. *Parastromateus niger* from Madagascar (Rakotofiringa et al. 1987).

Current host. *Kyphosus cinerascens* (Kiphoidae) (New host).

Site infection. Gills.

Specimens deposited. CHCM No. 541 (paratypes) (1 slide, 2 specimen).

Prevalence and mean intensity. 50 and 50 (n=2).

Remarks. This species was originally described as *Heteroplectanum parastromatei* by Rakotofiringa et al. (1987). However, Domingues and Boeger (2007) considered the genus *Heteroplectanum* as a junior synonym of *Acleotrema*. Therefore, this species was transferred to *Acleotrema* as *A. parastromatei*. It has a haptor with two squamodiscs, each consisting of 25 to 27 rows of sclerotised pieces. *A. parastromatei* in *K. cinerasens* from off Palmyra Atoll represents both a new host and a new geographical record. Only one host was found parasitised.

Polyopisthocotylea Odhner, 1912
Heteraxinidae Unnithan, 1957

Cemocotylella elongata (Meserve, 1938) Price, 1962

Type host. *Caranx melampygus* Cuvier (Carangidae).

Other host and localities. *Caranx melampygus* from Secas Island, Panama (Meserve 1938). *Xurel melampygus* (=*Caranx melampygus*) (Cuvier and Valenciennes) from Secas Island, Panama (Price 1962). *Caranx latus* Agassiz from Chetumal, Quintana Roo, Mexico (Bravo–Hollis and Salgado–Maldonado 1983) (all Carangidae).

Current host. *Caranx ignobilis* (Forsskål) (New host), *Caranx melampygus* and *Caranx papuensis* Alleyne and MacLeay (all Carangidae) (New host).

Site infection. Gills.

Specimens deposited. CHCM No. 536 (paratypes) (1 slide, 5 specimen).

Prevalence and mean intensity. *Caranx ignobilis* 50 and 7±7 (n=4), *Caranx melampygus* 16,7 and 4 (n=6) and *Caranx papuensis* 40 and 7±7 (n=5)

Remarks. Originally described as *Axine elongata* by Meserve (1938) from gills of *Caranx melampygus* (misidentified as *Xurel malampygus*). Price (1962) proposed the genus *Cemocotylella* to include *A. elongata,* changing the name of this species to *C. elongata*. *Axine elongata* (Meserve 1938) and *Heteraxine elongata* (Meserve 1938) Sproston 1946 are considered synonyms of *C. elongata*. This species is characterized by having an asymmetrical posterior haptor, four to five suckers on the short side and 24–25 on the long side, an unarmed genital atrium and MCO, and he absence of a vagina. The presence of *C. elongata* on *Caranx papuensis* from off Palmyra Atoll represents both a new host and a new geographical record.

Microcotylidae Taschenberg, 1879

Metamicrocotyla macracantha (Alexander, 1954) Koratha, 1955

Type host. *Mugil cephalus* Linnaeus (Mugilidae).

Other host and localities. *Mugil cephalus* from off Mexico (as *Microcotyle macracantha*) (Alexander 1954), the Gulf of California and Port Aransas, Texas from the same host (as *Metamicrocotyla macracantha*) (Koratha 1955), and *Mugil liza* from Brazil (as *Metamicrocotyla macracantha*) (Kohn et al. 1994). There are several reports of *Metamicrocotyla macracantha* from the USA on *M. cephalus* (Hargis 1956, Skinner 1975, 1978, Rawson 1976, Minchew 1977, Collins 1985), as well as from Australia (Young 1970), Mexico (Bravo–Hollis 1966, 1982, Juárez-Arroyo and Salgado-Maldonado 1989), Peru (Tantalean 1974), Puerto Rico (Garcia and Williams 1985), Chile (Oliva and Muñoz 1985, Bargiela 1987), and Venezuela (Conroy et al. 1985, 1986) from *Mugil curema* Valenciennes (all Mugilidae).

Current host. *Crenimugil crenilabris* (Forsskål) (Mugilidae) (New host).

Site infection. Gills.

Specimens deposited. CHCM No. 552 (paratypes) (1 slide, 1 specimen).

Prevalence and mean intensity. 4,8 and 3±1 (n=42).

Remarks: *Metamicrocotyla macracantha* is characterized by having a haptor separated from the body proper by a peduncle and with 26–67 clamps disposed in 2 symmetrical lateral rows. The shape of haptor varies depending on state of contraction and number of clamps. Clamps of microcotylid type, similar in shape, somewhat variable in size; middle clamps are the largest, and those from anterior and posterior ends are the smallest. Testes rounded, normally 16 to 25 in a zigzag line occupying inter-caecal space. The presence of *M. macracantha* from the gills of *Crenimugil crenilabris* off Palmyra Atoll represents both a new host and a new geographical record.

Pterinotrematidae Bychowsky & Nagibina, 1959

Pseudopterinotrema albulae Yamaguti, 1966

Type host. *Albula vulpes* Linnaeus (Albulidae).

Other host and localities. Yamaguti (1966) recorded *P. albulae* from *A. vulpes* off Hawai'i. It has also been found on the same host by Palm and Bray (2014) off Hawai'i.

Current host. *Albula glossodonta* (Forsskål) (Albulidae) (New host).

Site infection. Gills.

Specimens deposited. CHCM No. 535 (paratypes) (1 slide, 1 specimen), USNM No. 1459853 (voucher) (1 slide, 1 specimen).

Prevalence and mean intensity. 70,8 and 17±18 (n=24).

Remarks. *Pseudopterinotrema albulae* presents an asymmetrical, fan-shaped haptor on a posterior extension of the body proper, with nine pedunculate clamps. The clamps have very distinct features (see Yamaguti, 1968 for a detailed description of each clamp). MCO plug-shaped, with two unequal sclerotised filaments at base; genital pore ventromedial. The presence of *P. albulae* from *A. glossodonta* off Palmyra Atoll represents both a new host and a new geographical record.

Discussion

The species composition of monogeneans of the fishes from Palmyra Atoll is similar to that reported from other localities in the Indo-West Pacific and the Caribbean regions. These localities include the Great Barrier Reef (Australia), New Caledonia, Moorea (French Polynesia), South China Sea (Young 1968, Plaisance et al. 2004, Kritsky et al. 2009, Rehulkova et al. 2010) and Cuba (Zhukov 1976). Nine of the 16 species recorded in this study have been reported off Hawai'i (see Yamaguti 1968). This was not surprising, since Hawai'i is the closest location where monogeneans of marine fishes have been frequently examined. Some species recorded herein were previously considered endemic to Hawai'i; for example, *Pseudopterinotrema albulae*, *Benedenia hawaiiensis* and *Haliotrema minutospirale* (Palm and Bray 2014).

The absence of monogeneans from 26 of the 44 fish species examined was striking, even with relatively large sample sizes for some of those species (e.g. *Liza vaigiensis* n=54, *Valamugil engeli* n=63). Of those fishes that were infected, 14 of 18 species were parasitised by only one monogenean species. The low diversity of monogeneans found in our study is similar to that reported by Lafferty et al. (2008), who found only three species of monogeneans from five fish species captured on the forereef at Palmyra Atoll (n=11–25 individuals) and one monogenean species from a similar sample at the nearby Kiritimati Island. The species richness of monogeneans at Palmyra Atoll (16 monogenean species in 18 fish species) appears to be low compared with other localities, including the Hawaiian Islands, which are themselves remote and with some groups depauperate. Several host species from which monogeneans were absent in this study, have previous records of monogeneans. For example, *Pseudorhabdosynochus cupatus*, *P. melanesiensis*, *P. vagampullum* and *P. coioidesis* on *Epinephelus merra*; or *Pseudochauhanea sphyraenae* and *Vallisiopsis sphyraenae* on *Sphyraena barracuda*; or three *Haliotrema* species reported on *Stegastes nigricans* (Yamaguti 1968, Lo et al. 1998, Bu et al. 1999, Justine 2005, Hinsinger and Justine 2006).

The most likely hypothesis to account for the paucity of monogenean parasites at Palmyra Atoll is its geographical remoteness and small area. The Line Islands are isolated from other island groups in the Pacific and are also remote from the Austro-Malayan-Philippine region, the presumed centre of origin of Indo-West Pacific fishes and their parasites. Since there are also fewer species than those described from off Hawai′i, which is still further from the presumed centre of origin, we suggest the particularly small area of Palmyra Atoll contributes to the depauperate nature of its monogenean fauna. In fact, the low species richness of fishes from the Line Islands (Gosline 1971) is associated with the absence or scarcity of free-living species at Palmyra Atoll compared to other coral atolls in the Indo-West Pacific region (e.g. Adler 1992).

The presence of fish hosts, but often not their directly transmitted monogenean parasites, is consistent with the hypothesis that including a pelagic larval phase in marine animal life cycles is selectively advantageous because these small, morphologically and physiologically distinctive life history phases are incompatible with most of the parasites of juvenile and adult hosts (Strathmann et al. 2002).

This interspecific comparative study is consistent with the experimental studies (e.g., Grutter et al. 2011, 2017), that evaluate how parasites are transmitted to fish hosts after settlement from the pelagic region.

An additional explanation for the low number of monogenean species off Palmyra Atoll at local scale is related to the habitat from which almost all the fish examined were obtained: the lagoon flats. These flats are shallow and the daily temperature range is between 28.2 and 30.1°C (Koweek et al. 2014), perhaps offering an unsuitable environment for monogenean transmission or survival. For example, the negative effect of water temperature on the longevity and infection success of the oncomiracidia of *Neobenedenia* sp. infecting barramundi (*Lates calcarifer*) has been demonstrated (Hirasawa et al. 2010; Brazenor et al. 2013).

In conclusion, the number of species and individuals of monogeneans appear to be low in Palmyra lagoon-flat fishes. Filters acting at both local and biogeographical levels (*sensu* Holmes 1990, Combes 2001) seem to preclude the presence of a rich monogenean fauna. However, monogeneans were studied almost exclusively on fish from the lagoonal flats. The generally low infection prevalence is consistent with a more limited study of five fish species on coral reefs at Palmyra Atoll (Lafferty et al. 2008). Studies on the diversity of the coral reef fish fauna have found important differences in species number and composition between lagoonal flats, backreef and forereef zones (García-Sais 2010; Zhao et al. 2017). These ecological differences in reef zones could also contribute to differences in monogenean species richness and composition. Consequently, comparative studies of the monogenean fauna in different reef zones are needed to determine whether differences in monogenean diversity mirror differences in fish diversity. Palmyra Atoll has not had a permanent human population since WWII, and all fishing has been prohibited since it became a US National Wildlife Refuge in 2000. Consequently, the patterns and processes governing monogeneans diversity obtained in this relatively pristine environment could shed light on patterns of transmission prior to the removal of top predators by fishing, the situation found elsewhere.

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RESEARCH ARTICLE

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Earwigs from Brazilian caves, with notes on the taxonomic and nomenclatural problems of the Dermaptera (Insecta)

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Abstract

Based on samples collected during surveys of Brazilian cave fauna, seven earwig species are reported: *Cylindrogaster cavernicola* Kamimura, **sp. n.**, *Cylindrogaster* sp. 1, *Cylindrogaster* sp. 2, *Euborellia janeirensis*, *Euborellia brasiliensis*, *Paralabellula dorsalis*, and *Doru luteipes*, as well as four species identified to the (sub) family level. To date, *C. cavernicola* Kamimura, **sp. n.** has been recorded only from cave habitats (but near entrances), whereas the other four organisms identified at the species level have also been recorded from non-cave habitats. Wings and female genital structures of *Cylindrogaster* spp. (Cylindrogastrinae) are examined for the first time. The genital traits, including the gonapophyses of the 8th abdominal segment shorter than those of the 9th segement, and venation of the hind wings of Cylindrogastrinae correspond to those of the members of Diplatyidae and not to Pygidicranidae. This is the first synopsis of cave-dwelling earwigs of Brazil, one of the most species-rich areas of Dermaptera in the world.

Keywords

bat guano, cave fauna, *Cylindrogaster cavernicola* sp. n., Cylindrogastrinae, dermapteran taxonomy, female genitalia, *Heterolabis*, new synonym, traumatic mating

Introduction

Dermaptera (earwigs) is a polyneopteran insect order with more than 2000 described species from mainly tropical and warm temperate regions (Popham 2000; Grimaldi and Engel 2005; Haas et al. 2012). Although many dermapteran families have circumtropical distributions (Popham 2000), faunal, taxonomic, and ecological studies are scarce for tropical or subtropical species, especially the cave-dwelling species.

Organisms that live in the subterranean environments are frequently classified into three categories (e.g., Souza-Silva et al. 2011): i) trogloxenes - species occasionally found in caves or using the caves as nighttime or daytime shelters; ii) troglophiles – that could complete their whole life cycle inside or outside the caves; and iii) trogolobites species that do not occur in epigean habitats and exhibit behavioral, morphological and physiological specializations for exclusive survival within caves.

Only two troglobitic earwigs have been reported to date: *Anisolabis howarthi* Brindle, 1980 (Anisolabididae) of Hawaiian lava caves and *Anataelia troglobia* Martín and Oromi, 1988 (Pygidicranidae) of a lava cave in La Palma, Canary Islands. These species exhibit the characteristics of true cavernicolous insects, including reduced, apparently non-functional compound eyes, slender appendages, and a less-pigmented integument (Brindle 1980a; Martín and Oromi 1988). The genus *Anataelia* is endemic to the Canary Islands and the other two species, *A. canariensis* Bolivar, 1899 and *A. lavicola* Martín & Oromi, 1988, have well-developed eyes and are found both in subterranean and in epigean habitats (Ashmole and Ashmole 1987; Ashmole et al. 1992).

Haplodiplatys milloti (Chopard, 1940) (Haplodiplatyidae), which has been exclusively reported from an entirely dark part of an African cave, has well-developed compound eyes, while the integument is pale and the appendages are slenderer than in related species (Chopard 1940). It is estimated that this species recently adapted to cave life and has experienced minimal morphological changes (Brindle 1980a). Similarly, *Challia phoenix* Anisyutkin & Gorokhov, 1998 (Pygidicranidae sensu stricto) was described based on a single male specimen collected from a cave of Vietnam. Although its relationships to the cave habitat is unclear, according to the descriptions by Anisyutkin and Gorokhov (1998), this species shows no sign of reduction in the compound eye.

Conversely, eyeless earwigs do not necessarily occur in caves. *Anophthalmolabis* spp. (Anisolabididae) (Brindle 1968; Peck 1990) and *Caecolabia gomyi* Brindle, 1975 (Spongiphoridae) (Brindle 1975), are eyeless but usually found from soils. Peck (1990) reported that *Anophthalmolabis leleupi* Brindle, 1968, which is endemic to the Galapagos Islands, also occurs in caves (possibly troglophilic).

Members of the family Arixeniidae are also considered trogrophilic. These species are phoretic on bats (*Cheiromeles torquatus* Horsfield, 1824) or are found on bat guano (Nakata and Maa 1974; Marshall 1977). However, as the bat hosts roost in caves and tree hollows, arixeniids are not categorized as true cavernicolous animals. Nevertheless, they have reduced compound eyes as an adaptation to dark habitats (e.g., Nakata and Maa 1974). Similarly, in members of the Hemimeridae, which are phoretic on African tunnel-living giant rats (*Cricetomys* spp.), eyes are entirely absent (e.g., Nakata and Maa 1974). Morphological and molecular phylogenetic studies showed that both Hemimeridae and Arixeniidae are specialized in-groups of the superfamily Forficuloidea that also includes free-living earwigs of the families Spongiphoridae, Chelisochidae, and Forficulidae (Klass 2001; Haas and Klass 2003; Jarvis et al. 2005; Tworzydlo et al. 2013; Kocarek et al. 2013; Naegle et al. 2016).

Most earwigs found in caves are considered troglophiles that show no apparent specialization for life in dark environments (Chopard 1921, 1924; Brindle 1980a). Examples include *Chelisoches morio* (Fabricius, 1775) (Chelisochidae) and *Schizochelisoches brevipennis* (Borelli, 1923) (Chelisochidae) of Malaysian caves (Chopard 1929; McClure et al. 1967), and *Carcinophora americana* (Palisot de Beauvois, 1817) of Puerto Rican caves (Peck 1974).

As one of the most species-rich areas in the world, approximately 150 species of earwigs have been reported from Brazil (Haas 2012). Nevertheless, except for some rare mentions of Dermaptera in cave environments (Pinto-da-Rocha 1995), no comprehensive review has been reported for cave dermapteran fauna of this country. As an attempt to fill this gap, this is the first synopsis of Brazilian cave-dwelling earwig. Based on the samples collected during surveys of Brazilian cave fauna, we report seven earwig species from cave habitats for the first time. Wing and genital structures are described for some species, based on which we discuss their classification, ecology, and behavior.

Materials and methods

The 93 dermapteran specimens examined in this study were collected from 2000 to 2015 during surveys of Brazilian cave fauna. All samples were collected manually. Most caves were visited only once in the inventories of subterranean invertebrates conducted in different research projects. Several samples were collected by consulting companies or governmental institutions (ATIVO AMBIENTAL, CARSTE, SPELAYON, or CECAV), for which detailed environmental conditions of the locality are unknown.

All samples were preserved in 70% ethanol after collection, and therefore the body color of some specimens was bleached. To examine wing and genital structures, several adult samples were dried after mounting on cardboard using fish glue. Genitalia were removed from specimens, mounted in Euparal (Waldeck GmbH and Co. KG, Münster, Germany) between two coverslips, and attached to the pin of the respective specimen.

All of the samples examined in this study have been deposited in the Subterranean Invertebrate Collection of Lavras (ISLA), of the Universidade Federal de Lavras

(UFLA), Lavras, Brazil, with assignment of sample numbers shown in parentheses below, with the exception of some comparative samples from other depositories.

We follow Engel and Haas (2007) for the suprageneric classification, except for the subfamily Cylindrogastrinae which we considered to belong in Diplatyidae (see below). In addition, Engel et al. (2017) proposed to move the genus *Haplodiplatys*, which is considered the oldest offshoot of the extant Dermaptera (Haas 1995; Hass and Kukalová-Peck 2001; Hass and Klass 2003), from Diplatyidae to Haplodiplatyidae Engel, 2017. We follow this view. The generic classification follows that of Steinmann (1986, 1989a, 1989b, 1990, 1993) unless otherwise noted. The terminologies of Hass and Kukalová-Peck (2001), Klass (2003), and Kamimura (2014) were used for wing, female genital, and male genital structures, respectively.

Abbreviations

Male genitalia

dp	denticulated pad
ho	horn
pm	paramere
rsc	rectangular sclerite
tp	toothed plate
vg	virga

Female genitalia

ap	anal plate
gl9	gonoplac (=coxal lobe) IX
gp8	gonapophysis VIII
gp9	gonapophysis IX
lp	lateral plate
sa	spined area
sp	spermatheca
tg10	tergum X

Wing structures

AA3	anal anterior 3
AA4	anal anterior 4
AP	anal posterior
BAA1+2	anal anterior 1 + 2 basivenale (anal brace)
BAA3+4	anal anterior 3 + 4 basivenale
C	costa
CuA	cubitus anterior
CuP	cubitus posterior
FAJ	anojugal fulcalare
JA	jugal anterior

Depositories

ISLA	Invertebrados Subterrâneos de Lavras (Subterranean Invertebrates, Lavras) of UFLA
MM	Manchester Museum, UK
OMNH	Osaka Museum of Natural History, Japan
UFLA	Federal University of Lavras, Brazil
YK	personal collection of Y. K.

Results and remarks

Apart from *Cylindrogaster*, for which a new species is described, eight organisms were recorded in this study; however, only four were determined to the species level, while four were determined to the (sub)family level.

Order DERMAPTERA de Geer, 1773
Infraorder PROTODERMAPTERA Zacher, 1910
Family DIPLATYIDAE Verhoeff, 1902
Subfamily CYLINDROGASTRINAE Maccagno, 1929
Cylindrogaster Stål, 1855

Cylindrogaster cavernicola Kamimura, sp. n.

http://zoobank.org/CDD2C2A8-007B-4BF5-BCB7-B2C39D2427AC
Figs 1–7

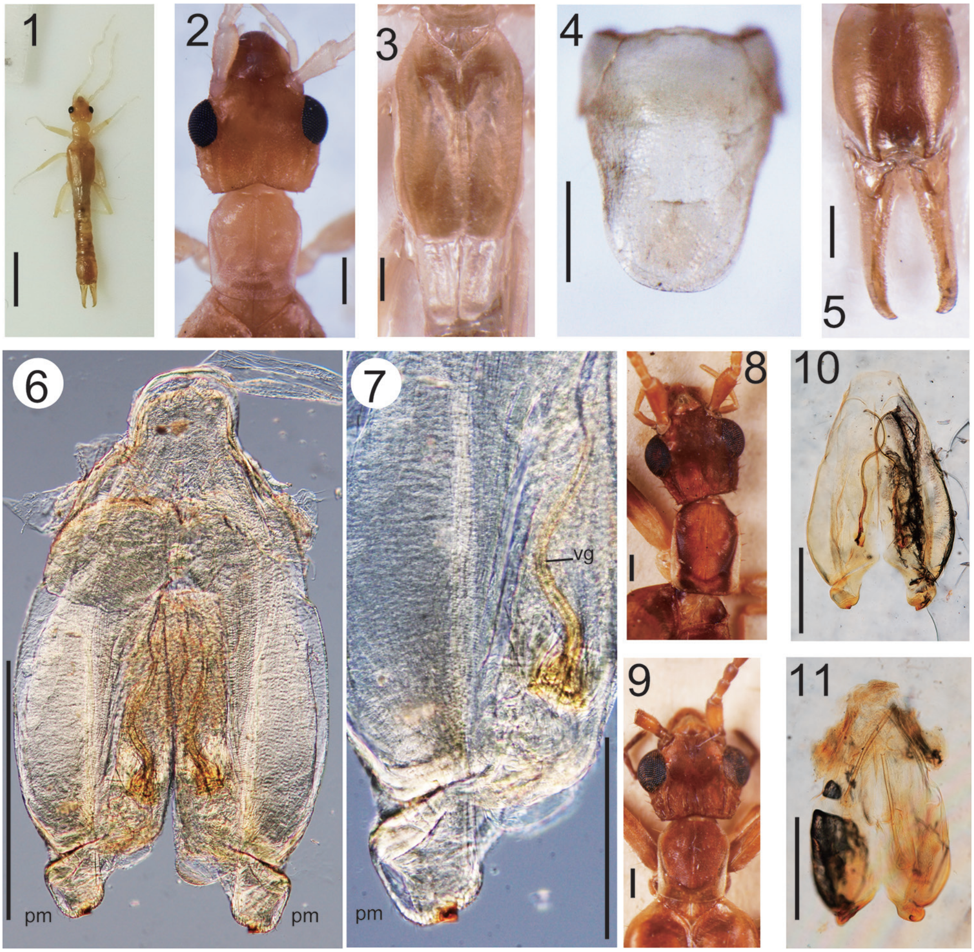
Material examined. Holotype ♂, 'Gruta Apertar | da Hora | Jandaíra RN <= Rio Grande do Norte>', 'ISLA | 21101', '15.ii.2010 | Ferreira, R.L. leg.', 'HOLOTYPE (male) | *Cylindrogaster cavernicola* | sp. n. | Det. Y. Kamimura 2017'.

Diagnosis. *Cylindrogaster cavernicola* sp. n. is a median-sized species with a slender abdomen and simple forceps. This species differs from all other species of *Cylindrogaster* with the combination of the following characters: the well-developed tegmina; pronotum slightly longer than broad; parameres with blunt apices; and short but weakly sinuated virgae.

Description. ***Male*** (holotype: Fig. 1). Length of body (without forceps): 11 mm. Length of forceps: 1.4 mm. Head width: 1.5 mm. Pronotum width: 1.0 mm. Pronotum length: 1.3 mm.

The body color of the holotype seems to have been bleached by preservation in ethanol. Body color uniformly pale amber but abdomen darker. Body, including forceps, sparsely pubescent.

Head (Fig. 2) slightly longer than broad, widest in the region of the eyes; frons tumid, occiput depressed; transverse and median suture not conspicuous but visible; hind margin strongly emarginated in middle; post-ocular carina well developed, almost straight, running from middle of the internal margin of the eyes to the hind margin of the head; lateral margins of post-ocular region bordered with strong bristles. Antennae broken, 10 (right) and 15 (left) segments remaining; first segment stout, expanded apically, length almost the same as the distance between antennal bases; second segment short, quadrate; third segment expanding apically, widest width almost the same as the length; fourth segment almost quadrate; fifth segment almost quadrate (left side) to 1.5 times longer than the width (right side); remaining segments gradually lengthening. Eyes prominent, slightly shorter than post-ocular length. Pronotum (Fig. 2) slightly longer than broad; anterior margin almost straight; sides parallel; hind margin broadly rounded; median sulcus distinct; prozona weakly raised. Tegmina (Fig. 3) well developed, 1.5 times wider than pronotum, about twice as long as pronotum; broad triangular scutellum visible. Wings (Fig. 3) well-developed. Legs long, slender; hind tarsi with first segment 2.5 times longer than third, second segment about half as long as third, claw with small arolium. Abdomen long, cylindrical; segments eight and nine slightly expanded. Penultimate (= 9th) sternite (Fig. 4) slender, with shallow concave sides; caudal margin forming



Figures 1–11. 1–7 *Cylindrogaster cavernicola* Kamimura, sp. n. (male, holotype): habitus (**1**), head and thorax (**2**), tegmina and wings (**3**), penultimate sternite (**4**), ultimate tergite and forceps (**5**), and genitalia (**6, 7**) **8, 10** *Cylindrogaster thoracicus* (MM 3637; collected from Itatiaia, Brazil; det. W. D. Hincks): head and thorax (**8**), and genitalia (**10**) **9, 11** *Cylindrogaster gracilis*: head and thorax (**9**: MM 3677; collected from Itatiaia, Brazil; det. W. D. Hincks), and genitalia (**11**: MM 3565; collected from Minas Gerais, Brazil; det. W. D. Hincks). Scale bars 3 mm for Fig. **1**; 0.5 mm for Figs **2–6, 8–11**; 200 µm for Fig. **7**.

a more or less semicircular lobe. Ultimate (= 10th) tergite (Fig. 5) moderately inflated, oval; caudal margin shallow concave between forceps. Forceps (Fig. 5) robust and short, almost straight, pubescent especially on inner margins, tapering and weakly curving inward apically, base of inner margin with small tooth. Genitalia (Figs 6, 7); virga short and sinuated; parameres (= external parameres) short and broad, rounded, with small triangular sclerotized tubercle and sparse short hairs at apex.

Female. Unknown.

Remarks. The subfamily Cylindrogastrinae consists of six species belonging to the Neotropical genus *Cylindrogaster* (Hincks 1955; Steinmann 1986, 1989b). Their external appearance resembles those of the Diplatyinae species or Diplatyidae *sensu stricto* (Table 1). However, males of *Cylindrogaster* spp., including *C. cavernicola* sp. n. described here, have one gonopore on each of the paired virgae, which is a heavily sclerotized process containing the terminal part of the ejaculatory duct, whereas male diplatyids (and haplodiplatyids) have a pair of bifurcated virgae (Hincks 1955; Steinmann 1989a).

This new species is allied to *C. gracilis* Stal, 1855, which was recorded from Brazil (and also possibly from Peru). However, the virga is entirely straight and the parameres are much wider than the length in the latter species (Fig. 11). Another Brazilian species, *C. thoracicus* Dohrn, 1863, can be distinguished from *C. cavernicola* sp. n. by its much longer virgae (Fig. 10) and pronotum (Fig. 8).

Key to the known *Cylindrogaster* species (males only)

1 Tegmina reduced to small lateral flaps. Ultimate tergite strongly inflated. Forceps well developed, so-called macrolabic............ ***Cylindrogaster bicyclurus***

– Tegmina not reduced, well developed, normal. Ultimate tergite not or little inflated. Forceps, so-called microlabic.. **2**

2 Parameres of genitalia triangular with pointed apex **3**

– Parameres of genitalia trapezoid or oval, broader than long, with blunt apex..... **4**

3 Virga short but sinuated, with a characteristic projection at middle .... ***Cylindrogaster sahlbergi***

– Virga short, curved but not sinuated, without a characteristic projection at the middle .... ***Cylindrogaster yepezi***

4 Pronotum (excluding anterior zone tapering to head) apparently longer than broad (Fig. 8).. **5**

– Pronotum (excluding anterior zone tapering to head) almost quadrate or slightly longer than broad (Figs 2, 9).. **6**

5 Pronotum (excluding anterior tapering region) more than 1.5 times longer than broad. Virga straight, very short, almost half as long as penis lobe......... .... ***Cylindrogaster velox***

– Pronotum (excluding anterior tapering region) less than 1.5 times longer than broad. Virga sinuated, relatively long (Fig. 10).................................... .... ***Cylindrogaster thoracicus***

6 Virga simple, straight, almost as long as penis lobe (Fig. 11) .... ***Cylindrogaster gracilis***

– Virga very short, almost half as long as penis lobe, but weakly sinuated (Figs 6, 7).................................... ***Cylindrogaster cavernicola* Kamimura, sp. n.**

Etymology. The species epithet refers to the cave-dwelling habit of this new species, although it is presently unknown whether it is a troglobite.

Distribution. Rio Grande do Norte, Brazil.

Table 1. Proposed classification systems for the infraorder Protodermaptera Zacher, 1910.

Hincks (1955, 1959)	Popham (1985)	Steinmann (1986, 1989b)	Sakai (1996)	Engel and Haas (2007)	This study
Pygidicranidae	**Pygidicranidae**	**Pygidicranidae**	**Pygidicranidae**	**Pygidicranidae**	**Pygidicranidae**
Anataeliinae	Anataeliinae	Anataeliinae	Anataelinae	Anataeliinae	Anataelinae
Blandicinae	Blandicinae	Blandicinae	Blandicinae	Blandicinae	Blandicinae
		Brindlensiinae	Brindlensiinae	Brindlensiinae	Brindlensiinae
	Chaliinae	Challiinae	Chaliinae	Challiinae	Chaliinae
Echinosomatinae	Echinosomatinae	Echinosomatinae	Echinosomatinae	Echinosomatinae	Echinosomatinae
			Prolabiscinae	(= Prolabiscinae)	Prolabiscinae
Esphalmeninae	Esphalmeninae	Esphalmeninae	Esphalmeninae	Esphalmeninae	Esphalmeninae
Pygidicraninae	Pygidicraninae	Pygidicraninae	Pygidicraninae	Pygidicraninae	Pygidicraninae
Pyragrinae	Pyragrinae	Pyragrinae	Pyragrinae	Pyragrinae	Pyragrinae
				Diplatymorphinae	
				Cylindrogastrinae	
Karschiellinae	Karschiellinae	Karschiellinae	Karschiellinae	**Karschiellidae**	**Karschiellidae**
					Haplodiplatyidae (*sensu* Engel et al. 2017)
			Diplatyidae (*sensu lato*)	**Diplatyidae** (*sensu stricto*)	**Diplatyidae**
Diplatyinae	Diplatyinae	Diplatyinae	Diplatyinae		Diplatyinae
		Diplatymorphinae	(= Diplatymorphinae)		Diplatymorphinae
(= Cylindrogastrinae)	(= Cylindrogastrinae)	Cylindrogastrinae	Cylindrogastrinae		Cylindrogastrinae

Association with caves. The specimen of *Cylindrogaster cavernicola* Kamimura, sp. n. was collected near the entrance of a cave associated with limestone rocks from the Jandaíra formation (Upper Cretaceous) in northern Rio Grande do Norte state. The caves in this region are predominantly shallow, most of which present several connections with the epigean environment (usually vertical cracks in the limestone outcrops). Accordingly, many caves in the area are strongly influenced by the external environment. Even so, given the extremely dry external environment, the caves represent a more suitable habitat for many animal species, presenting more stable temperatures and higher humidity than the epigean habitat. Furthermore, although the macro-caves are more influenced by the epigean environment, they are connected to huge systems of meso-caves, comprising small passages that are much more stable.

Cylindrogaster sp. 1
Figs 12–17

Material examined. 1 ♀, Gruta Túneis, Lagoa Santa, Minas Gerais, 10.x.2011, Ferreira, RL leg. (ISLA 43365).

Association with caves. The female specimen was collected near the entrance of a cave of the Sumidouro state park, located in Lagoa Santa, Minas Gerais state. Numerous nymphs presumably belonging to this species were observed throughout the years, especially on the cave walls in areas close to entrances, in the limestone caves of this region. Therefore, it is possible that this species uses the caves as a protected habitat during its development, but leaves the caves when reaching adulthood. They probably prey upon small invertebrates that are found on the walls near the entrances.

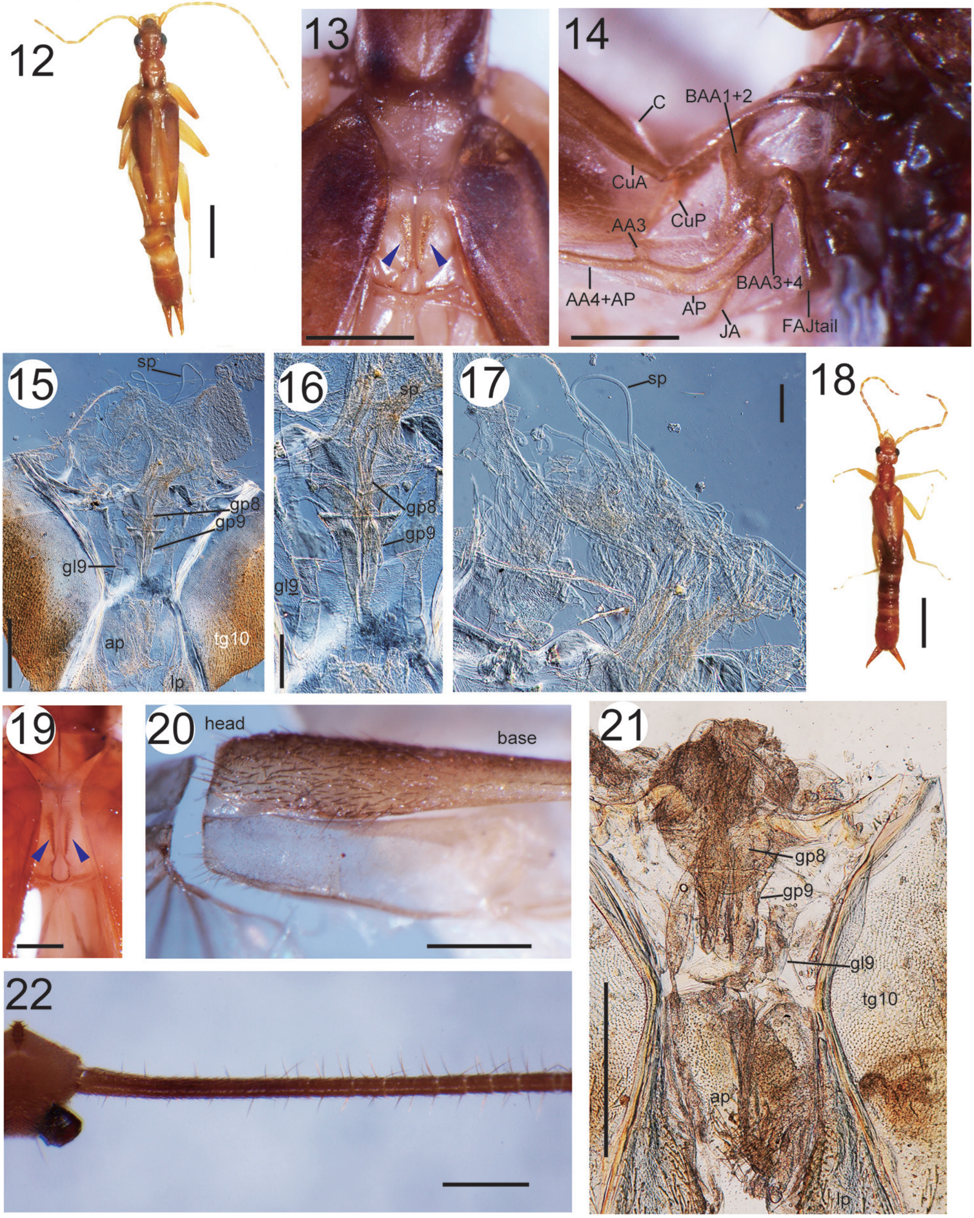
Description and remarks. In this study, two adult females of *Cylindrogaster* were examined. Based on differences in body size and genital structures (see below), these two females are not conspecific. The characteristics for species diagnosis have not been established for female *Cylindrogaster* spp. In addition, because the collection localities of both female samples (from Minas Gerais and Pará states, respectively) are quite far from the type locality of *C. cavernicola* sp. n. (Rio Grande do Norte state), these female samples are tentatively treated as *Cylindrogaster* sp. 1 (Figs 12–17) and *Cylindrogaster* sp. 2 (Figs 18–21) in this study.

Wing and female genital structures have not been reported for any members of *Cylindrogaster*. The female genital region of *Cylindrogaster* sp.1 is characterized by having shorter gonapophysis VIII (**gp8)** than gonapophysis IX (**gp9**), which was slightly shorter than the finger-like gonoplac IX (**gl9**) (Figs 15–17).

The spermatheca of *Cylindrogaster* sp. 1 consisted of long thin tubes (Fig. 17) without sclerotized or pigmented spermathecal capsules. In the infraorder Protodermaptera (= Pygidicranidae *sensu lato* or sometimes referred to as basal dermapterans), the number of spermatheca and internal branches vary both inter- and intraspecifically (Popham 1965a; Klass 2003; Kamimura 2004). However, poor specimen quality prevented characterization of the *Cylindrogaster* sp. 1 spermatheca.

According to Hass and Kukalová-Peck (2001), Diplatyidae (*Diplatys*) and Haplodiplatyidae (*Haplodiplatys*) are separated from other members of the infraorder Protodermaptera by the presence of (1) a narrow, slender, and elongated fustis head, (2) a long and slender costal area, (3) a concave and strongly three-dimensional anojugal arm (FAJ: anojugal fulcalare), (4) the distal end of CuA3+4 (cubitus anterior 3 and 4) lying between the 8th and 9th branches of AP1+2 (anal posterior 1 and 2), and (5) two proximal branches of AP1+2 diverging close together. The characteristics unique to Diplatyidae and Haplodiplatyidae (1–3) were observed in *Cylindrogaster* sp. 1 (Fig. 14). The latter two traits were not observed as the poor quality of the specimen prevented opening of the wings.

The genus *Haplodiplatys* (Haplodiplatyidae) is characterized by multiple plesiomorphic features, including laterally symmetrical tegmina and absence of a spiny ridge (a component of the tegmina-locking device) on the dorsal side of the mesothorax (Hass and Kukalová-Peck 2001). The female sample of *Cylindrogaster* sp. 1, however, possessed well-developed spiny ridges (Fig. 13), similar to those in *Diplatys* spp. (Diplatyidae).



Figures 12–22. 12–17 *Cylindrogaster* sp. 1 (female): habitus (**12**), spiny ridges (indicated by the blue arrowheads) on the mesothorax (**13**), wing base of the left hindwing (**14**), and genital regions (**15–17**) **18–21** *Cylindrogaster* sp. 2 (female): habitus (**18**), spiny ridges (indicated by the blue arrowheads) on the mesothorax (**19**), fustis of the left hindwing (**20**), and genital regions (**21**) **22** *Cylindrogaster* sp. (nymph): detail of cercus. Scale bars 3 mm for Figs **12, 18**; 0.5 mm for Figs **13–15, 19–22**; 200 μm for Figs **16, 17**.

Cylindrogaster sp. 2

Figs 18–21

Material examined. 1 ♀, Cave N5SM1-017, Parauapebas, Pará, 17.ii.2011, CARSTE leg. (ISLA 15558).

Association with caves. The specimen was found in the cave N5SM1-017 (also known as GEM-1190 cave). This cave consists of a shallow iron ore cave (14 m horizontal projection), located in Carajás region (Pará state, Brazil). The surrounding vegetation is composed of Amazon forest with a dense canopy. The cave has only one wide and shaded entrance, with the presence of vegetation (lichens, moss, and ferns). Furthermore, it does not present an aphotic zone, being lightened throughout its whole extension. The litter is abundant near the entrance zone and sparse in the rest of the cavity. Several caves were sampled in this region, and as a single specimen was found, it is likely that this species is accidental or seeks only temporarily shelter in caves.

Description and remarks. The genital structures of this species are essentially similar to those of *Cylindrogaster* sp. 1, but the spermatheca was missing likely due to incorrect dissection. *Cylindrogaster* sp. 2 differs from *Cylindrogaster* sp. 1 in having triangular shaped **gl9** (Fig. 21) vs. finger-like in *Cylindrogaster* sp. 1 (Figs 15, 16), as well as a much smaller body size (Fig. 18 vs. 12). The wing and mesothoracic structures of *Cylindrogaster* sp. 2 were basically the same as those of *Cylindrogaster* sp. 1. Refer to Figures 19 and 20 for images of the spiny ridges and fustis, respectively.

Cylindrogaster species

Fig. 22

Material examined. 1 nymph, Cavidade RF 86, Barão de Cocais, Minas Gerais, 9.ii.2015, ATIVO AMBIENTAL leg. (ISLA 15507) – 1 nymph, Cavidade CBT_09, Barão de Cocais, Minas Gerais, 19.i.2015, ATIVO AMBIENTAL leg. (ISLA 15508) – 1 nymph, S11D, S11D-0003, Serra / Sul, Canaã dos Carajás, Pará, 16.xii.2014, CARSTE leg. (ISLA 17201) – 1 nymph, Gruta da Lapinha, Lagoa Santa, Minas Gerais, 7.vii.2011, Ferreira, RL leg. (ISLA 21083) – 3 nymphs, Cave GEM-1194, Parauapebas, Pará, 23.ii.2011, CARSTE leg. (ISLA 21087) – 1 nymph, CAPA 03, Itabirito, Minas Gerais, 11.xi.2013, SPELAYON leg. (ISLA 21088) – 1 nymph, Cave Mll GEM-1705, Parauapebas, Pará, 13.iv.2011, CARSTE leg. (ISLA 21091) – 2 nymphs, Cave Mll GEM-1738, Parauapebas, Pará, 3.xi.2011, CARSTE leg. (ISLA 21092) – 1 nymph, Cave Mll GEM-1694, Parauapebas, Pará, 20.iii.2011, CARSTE leg. (ISLA 21095) – 4 nymphs, Didi Vieira cave, Afonso Cláudio, Espírito Santo, 23.iii.2005, Souza MS et al. leg. (ISLA 21098) – 1 nymph, Sitio Paraíso cave, Ecoporanga, Espírito Santo, 22.vii.2004, Souza MS et al. leg. (ISLA 21099) – 2 nymphs, Gruta do Roxo, Novo Oriente de Minas, Minas Gerais, 20.vii.2002, Souza MS et al. leg. (ISLA 21100) – 1 nymph, SEP-0407 (Geraldo Gusso), Felipe Guerra, Rio Grande do Norte, 2.x.2010, Ferreira, RL leg. (ISLA 21102) – 1 nymph, Lapa de Urtiga, Vazante, Minas Gerais, 16.ix.2010, Ferreira, RL leg. (ISLA 2735).

Remarks. A total of 21 nymphs of *Cylindrogaster* were examined. Nymphal cerci were frequently lost in these specimens, but when present, they were always segmented instead of unsegmented forceps of adults (Fig. 22).

Species diagnosis has not been established for nymphal samples of *Cylindrogaster* spp.

Infraorder EPIDERMAPTERA Engel, 2003
Family ANISOLABIDIDAE Verhoeff, 1902
Subfamily ANISOLABIDINAE Verhoeff, 1902
Euborellia Burr, 1910

Euborellia janeirensis (Dohrn, 1864)

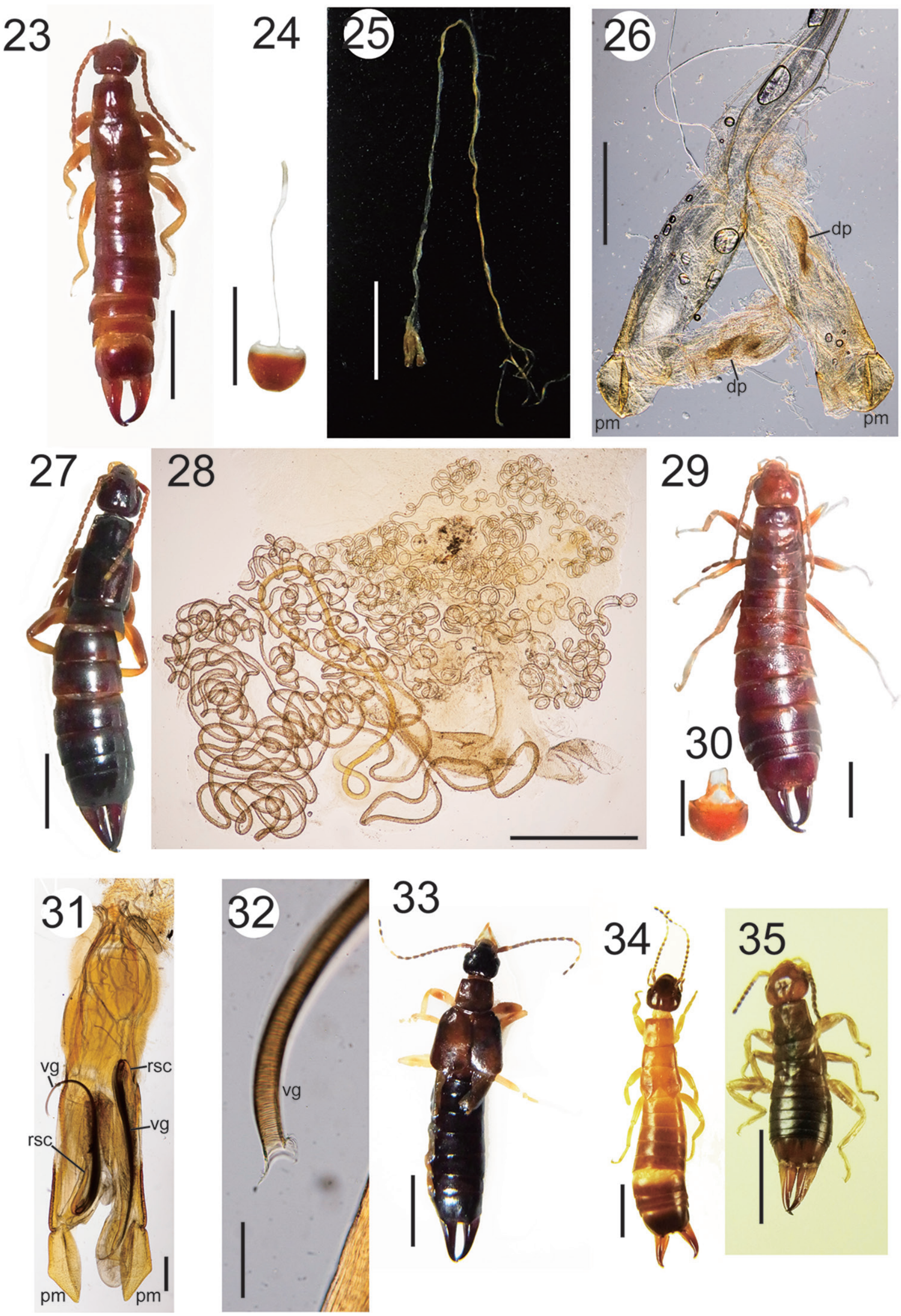
Figs 23–28

Material examined. 3 ♂♂, 6 ♀♀, 7 nymphs, Gruta dos Farias cave, Barbalhas, Ceará, 30.iv.2007, Ferreira, RL leg. (ISLA 15565) – 1 nymph, Cave GEM-1623, Parauapebas, Pará, 16.iii.2011, CARSTE leg. (ISLA 21085) – 1 nymph, Gruta Ecos cave, Cocalzinho de Goiás, Goiás, 4.iv.2006, CECAV leg. (ISLA 21096).

Association with caves. While most earwigs found in Brazilian caves seem to be accidental, this species was present as a large population within Gruta dos Farias cave, a sandstone cave located in Barbalhas municipality (Ceará state, Brazil). Many adults and nymphs were observed only in guano piles in deeper areas of the cave, which has a stream trespassing its entire conduit, strongly suggesting that the population is troglophilic. They are likely feeding on bat guano or preying upon small invertebrates.

Description and remarks. All adult specimens examined in this study had fully developed tegmina, but lacked hind wings. Four species of *Euborellia* from the Neotropical region, *E. boliviana* Brindle, 1971, *E. ambigua* (Borelli, 1906), *E. caraibea* Hebard, 1921, and *E. janeirensis*, also have such characteristics. Among these species, *E. janeirensis* is distinguished from the others by the presence of well-developed lateral longitudinal ridges on the male abdominal tergites VI and IX, and one or more white/yellow distal antennal segments (Steinmann 1989a). The external morphologies and male genitalia of the specimens examined in this study agreed well with those described previously for *E. janeirensis*, including brown markings on the femora (Figs 23 and 27), the shapes of the forceps (Figs 23 and 27), and the shapes of the parameres and denticulated pads in the penis lobe (Fig. 26).

Taxonomists generally examine only the terminal region of the male genital organs. The male genitalia of *E. janeirensis* were approximately 22 mm in length, and more than twice the body length with forceps (Fig. 25). The manubrium, which is an extension in the basal, inner margin of the penultimate sternite (Burr 1915b; Ramamurthi 1958), was approximately 6 mm in length (Fig. 24). In male earwigs, the



Figures 23–35. 23–26 *Euborellia janeirensis* (male): habitus (**23**), penultimate sternite + manubrium (**24**), and genitalia (**25, 26**) **27–28** *Euborellia janeirensis* (female): habitus (**27**), and spermatheca (**28**) **29–32** *Euborellia brasiliensis* (male): habitus (**29**), penultimate sternite + manubrium (**30**), and genitalia (**31, 32**) **33** Anisolabididae gen. sp. 1 (female): habitus **34** Anisolabididae gen. sp. 2 (nymph): habitus **35** Anisolabididae gen. sp. 3 (nymph) habitus. Scale bars 3 mm for Figs **23–25, 27, 29, 30, 33–35**; 0.5 mm for Figs **26, 28, 31**; 100 µm for Fig. **32**.

retractor muscles of the genitalia originate from this structure (Popham 1965a). As reported by Mariani (1994), the spermatheca of this species was a long and thin blind duct lacking a capsule at the distal end (Fig. 28).

Males of *Euborellia* spp. directly insert the elongated virga into the female spermatheca during copulation (Kamimura 2000; Lieshout and Elgar 2011). Elongation of the virga (and the genitalia as a whole, which functions as the virgal sheath when in repose) is considered an adaptation for removal of rival sperm from the female spermatheca, which is usually longer than the virga (Kamimura 2000, 2005, 2013, 2015; Lieshout and Elgar 2011). Thus, genital elongation in *E. janeirensis* suggests intensive sperm competition in this species.

Distribution. Brazil, Argentina, Paraguay, and Venezuela.

Euborellia brasiliensis (Borelli, 1912)

Figs 29–32

Material examined. 2 ♂♂, 2 nymphs, Gruta dos Coelhos cave, Lima Duarte, Minas Gerais, 11.vii.2005, Ferreira, RL leg. (ISLA 15564).

Association with caves. This species was found in deeper areas (aphotic zones) of Gruta dos Coelhos and Gruta do Pião caves, both associated with quartzite rocks and located in the Ibitipoca state park (Lima Duarte municipality, Minas Gerais state, Brazil). In the latter cave, several individuals were found walking near root masses, probably searching for prey. There are several caves in the area, and at least three distinct inventories of cave fauna were performed over the last 10 years. However, this species was only found in two caves, suggesting that, although probably not accidental, their association with subterranean habitats is uncommon.

Remarks. This apterous anisolabidid species from Brazil (Fig. 29) was originally described as *Heterolabis brasiliensis* by Borelli (1912), as the type species of the monotypic genus *Heterolabis*. Popham and Brindle (1966) recognized the type species as a member of the genus *Euborellia* Burr, 1910 and proposed the combination *Euborellia brasiliensis* (Borelli, 1912) Popham & Brindle, 1966. Therefore, they considered the generic name *Heterolabis* as a synonym of *Euborellia*. Their decision was followed by Reichardt (1968b), Sakai (1970), and Steinmann (1977, 1978).

Srivastava (1978) described a second species belonging to *Heterolabis*, i.e. *Heterolabis punctata* Srivastava, 1978. Its transfer to the genus *Euborellia* was proposed by Sakai (1982, 1987) and Srivastava (1999). Since the binomen *Euborellia punctata* was preoccupied by *Euborellia punctata* Borelli, 1927, they proposed the replacement names *Euborellia srivastavai* Sakai, 1987 and *E. mindanoensis* Srivastava, 1999, respectively. An alternative generic position for *H. punctata* was proposed by Steinmann (1989b); who recognized it as a member of the genus *Epilabis* Burr, 1915. Since the relevant binomen was preoccupied by *Epilabis punctata* Srivastava, 1976, he proposed the replacement name *Epilabis harlequin* Steinmann, 1989.

Currently *Heterolabis* Borelli, 1912 is considered a synonym of *Euborellia*, and the species previously considered as members of *Heterolabis* is as follows:

1. *Euborellia brasiliensis* (Borelli, 1912): Popham and Brindle (1966)
   Synonym: *Heterolabis brasiliensis* Borelli, 1912
2. *Euborellia srivastavai* Sakai, 1987
   Synonyms: *Heterolabis punctata* Srivastava, 1978; *Epilabis harlequin* Steinmann, 1989 (junior objective synonym); *Euborellia mindanoensis* Srivastava, 1999 (junior objective synonym).

The generic name *Heterolabis* Borelli, 1912 is an invalid homonym of *Heterolabis* Kriechbaumer, 1889 (Ichneumonidae).

Distribution. Brazil.

Anisolabidinae sp. 1

Fig. 33

Material examined. 1 ♀, cave SERP 0100, Conceição do Mato Dentro, Minas Gerais, 26.v.2014, SPELAYON leg. (ISLA 15557).

Association with caves. Unknown.

Remarks. The tegmina and wings were fully developed (Fig. 33), and this species may belong to the genus *Carcinophora* Scudder, 1876.

Anisolabidinae sp. 2

Fig. 34

Material examined. 2 nymphs, Gruta Ecos cave, Cocalzinho de Goiás, Goiás, 4.iv.2006, CECAV leg. (ISLA 21097) – 1 nymph, Cave GEM-1710, Parauapebas, Pará, 14.iii.2011, CARSTE leg. (ISLA 21086) – 1 nymph, cave SERP 0100, Conceição do Mato Dentro, Minas Gerais, 26.v.2014, SPELAYON leg. (ISLA 21082).

Association with caves. Unknown.

Remarks. Four nymphs, with well-developed wing primordia and some whitish antennal segments, were examined. Being recorded from Goiás, Pará, and Minas Gerais states, this species is possibly distributed widely in Brazil. Otherwise, several species may be mixed in this tentative species.

Anisolabidinae sp. 3

Fig. 35

Material examined. 1 nymph, cave RF 103, Barão de Cocais, Minas Gerais, 16.i.2015, ATIVO AMBIENTAL leg. (ISLA 15505).

Association with caves. Unknown.

Remarks. Only one young nymphal specimen was collected. This species is characterized by a brownish stripe straddling the long axis of the compound eye.

Family SPONGIPHORIDAE Verhoeff, 1902

Spongiphoridae sp. 1

Material examined. 1 nymph, Cave Mll GEM 1712, Parauapebas, Pará, 30.x.2011, CARSTE leg. (ISLA 21093).

Association with caves. Unknown.

Remarks. This species is tentatively assigned to the family Spongiphoridae. Only one young nymph, which lacked the post-abdomen including the forceps, was examined. The antennae are characteristically stout.

Subfamily LABIINAE Burr, 1911

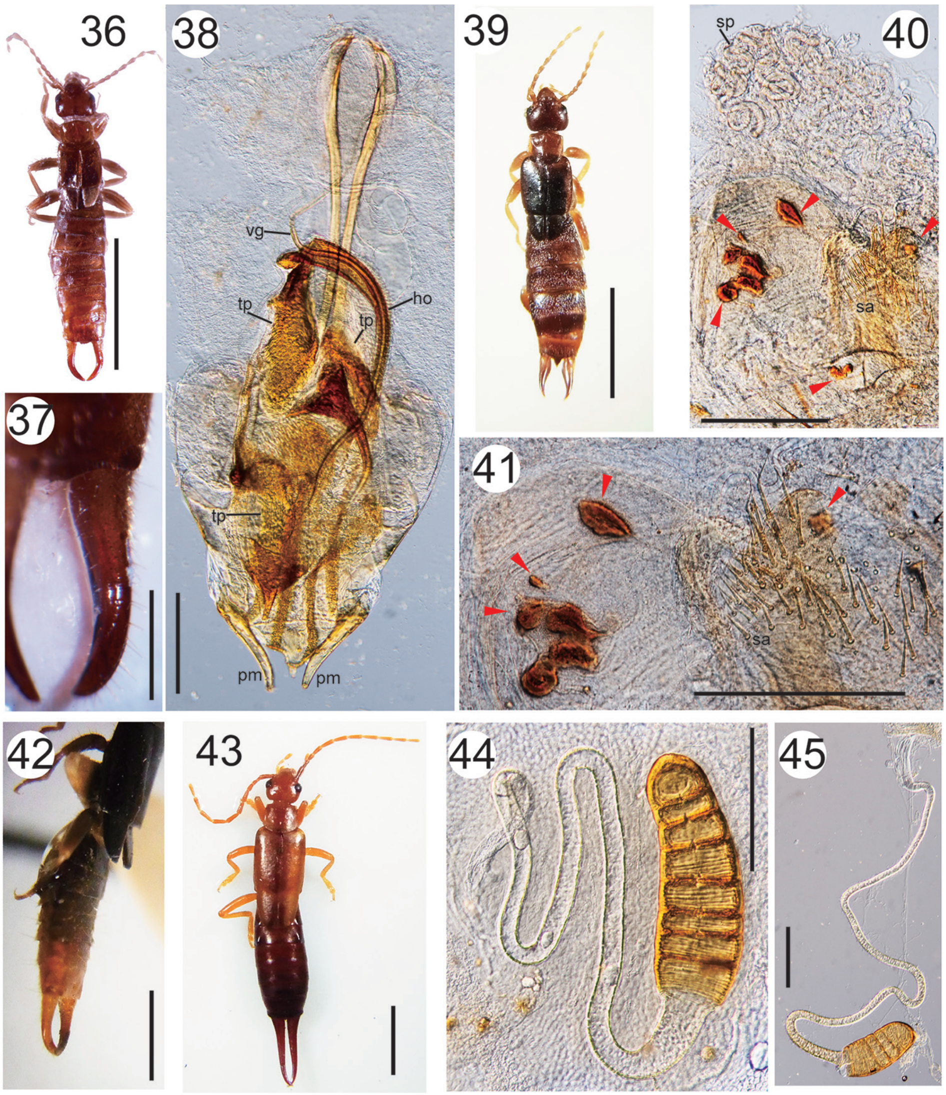
Paralabellula Kevan, 1997 (= *Paralabella* Steinmann, 1990; see Kevan and Vickery 1997)

Paralabellula dorsalis (Burmeister, 1838)

Figs 36–42

Material examined. 2 ♂♂, 9 ♀♀, 8 nymphs, Cave N5SM2-099 (= GEM-1799 cave), Parauapebas, Pará, 5.v.2011, CARSTE leg. (ISLA 15563) – 1 ♀, Cave N5SM2-019 (= GEM-1739 cave), Parauapebas, Pará, 31.x.2010, CARSTE leg. (ISLA 15562) – 3♀, Cave N5SM2-099 (= GEM-1799 cave), Parauapebas, Pará, 31.x.2010, CARSTE leg. (ISLA 15560) – 1 ♂, 2 ♀♀, 8 nymphs, Cave N5SM2-019 (= GEM-1739 cave), Parauapebas, Pará, 5.v.2011, CARSTE leg. (ISLA 15561) – 1 nymph, Cave N5SM2-019 (= GEM-1739 cave), Parauapebas, Pará, 31.x.2010, CARSTE leg. (ISLA 21084) – 1 nymph, Cave N5SM2-019 (= GEM-1739 cave), Parauapebas, Pará, 5.v.2011, CARSTE leg. (ISLA 21089) – 1 nymph, Cave N5SM2-019 (= GEM-1739 cave), Parauapebas, Pará, 5.v.2011, CARSTE leg. (ISLA 21090) – 3 nymphs, Cave N5SM2-019 (= GEM-1739 cave), Parauapebas, Pará, 31.x.2010, CARSTE leg. (ISLA 21094).

Association with caves. Many specimens of *P. dorsalis* were found in two iron ore caves (N5SM2-019 cave – synonym of GEM-1739 cave, and N5SM2-099 cave – synonym of GEM-1799 cave), both located in Carajás region (Pará state). These caves occur in an iron ore plateau surrounded by the Amazon forest. However, they are in an area of metallophilic savannah, a vegetation type usually found at the top of plateaus. The caves are considerably large (> 100 m in horizontal projection) compared to other caves in the area. Although many caves were sampled in the plateau (at least 100 caves), this species was found in only these two caves, which contain huge colonies of the insectivorous bat genus *Pteronotus* (*Pteronotus gymnonotus* Wagner, 1843, in the N5SM2-019 cave and *Pteronotus parnellii* (Gray, 1843) in the N5SM2-099 cave). These colonies produce large guano piles, where several individuals of *P. dorsalis* were



Figures 36–45. 36–38 *Paralabellula dorsalis* (male): habitus (**36**), forceps (dorsolateral view) (**37**), and genitalia (**38**) **39–41** *Paralabellula dorsalis* (female): habitus (**39**), spermatheca and spiny area in the genitalia (**40, 41**). Repaired wound patches are indicated by the red arrowheads in Figs 40 and 41 **42** *Paralabellula dorsalis* (male; a specimen from Colombia, det. A. Brindle; OMHH S. Sakai Collection, 31.iii.2002 [01-25]): abdomen and forceps (dorsolateral view) **43–44** *Doru luteipes* (female): habitus (**43**), and spermatheca (**44**) **45** *Doru lineare* (female; coll. Y. Kamimura, at Varzelândia, Minas Gerais, Brazil, outside of caves on 13.iii.2016): spermatheca. Scale bars 3 mm for Figs **36, 39, 42, 43**; 0.5 mm for **37**; 200 µm for Figs **38, 40, 41, 44, 45**.

observed. The populations of *P. dorsalis*, which include both adults and nymphs, were observed in both dry and rainy seasons in the two caves, strongly suggesting that they are troglophilic.

Description and remarks. The external morphologies and genital structures of male and female specimens were examined (Figs 36–41) and matched those of *Paralabellula dorsalis* (Burmeister 1838; Brunner 1906; Brindle 1971a,b,c; Steinmann 1989a; Briceño 1997; Eberhard et al. 1998). Winged and wingless morphs have been reported for a Costa Rican population of this species, where wingless individuals always predominated in the wild (Briceño and Eberhard 1987). Significantly more winged adults emerged when nymphs were subjected to low nutritional conditions (Briceño and Eberhard 1987). All adults (3 males and 13 females) examined in this study were winged morphs with fully developed tegmina and hind wings (Figs 36, 39). These findings may have been due to the poor nutritional conditions in caves. Although previous authors noted that each branch of the male forceps has a small inner tooth at the base (see Brindle 1971a, b, c; Sakai 1993), all males (n = 3) examined in this study lacked this tooth (Fig. 37). However, one male specimen from Moniquira, Colombia, determined by A. Brindle, also lacked a tooth at the base of the forceps (Fig. 42).

Based on samples collected from Costa Rica, Briceño (1997) reported the detailed genital structures of this species, which included a horn-like structure and several heavily sclerotized toothed plates in the penis lobe. These structures were also found in the three male samples examined in this study (**ho** and **tp**, respectively, in Fig. 38). The spermatheca of this species is a long, thin, blind duct lacking a capsule at the distal end (Mariani 1994; Briceño 1997). Briceño (1997) also reported the presence of multiple fine spines around the spermathecal opening. All such features were present in the specimens examined in this study (Fig. 40, 41).

Using specimens fixed during copulation, Briceño (1997) also examined coupling of the male and female genitalia. Toothed plates were exposed by eversion of the inflated penis lobe, and contacted the inner walls of the vagina, including the spiny area. The horn-like structure functioned as a guiding sheath for the virga, potentially to facilitate insertion into the female spermatheca. There is accumulating evidence that many male animals inflict wounds on the female during mating through use of their genital structures (Lange et al. 2013; Tatarnic et al. 2014; Reinhardt et al. 2014). However, this mode of mating, termed traumatic mating, has been reported in only two species of earwigs, *Echinosoma denticulatum* Hincks, 1959 (Pygidicranidae: Echinosomatinae; Kamimura and Lee 2014a) and *Marava arachidis* (Yersin, 1860) (Spongiphoridae: Spongiphorinae; Kamimura et al. 2016b). While Briceño (1997) failed to mention the occurrence of copulatory wounding in *P. dorsalis*, melanized patches on the membranous region at the spermathecal opening were observed in this study (n = 2; Figs 40, 41). This finding suggests that the male genitalia cause wounding during copulation.

Distribution. West Indies, Mexico, Costa Rica, Panama and northern South America (including Brazil).

Family FORFICULIDAE Latreille, 1810
Subfamily FORFICULINAE Latreille, 1810
Doru Burr, 1907

Doru luteipes (Scudder, 1876)
Figs 43, 44

Material examined. 1 ♀, Gruta do Vento cave, Pains, Minas Gerais, 12.x.2000, R. L. Ferreira leg. (ISLA 495) – 1 ♀, Gruta Zé Geraldão cave, Pains, Minas Gerais, 10.iii.2009, R. A. Zampaulo leg. (ISLA 534).

Association with caves. *Doru luteipes* is an extremely common species in Brazil (Reis et al. 1988), being frequently associated with crops, especially corn. The few observed specimens were found from the Pains region, which is considered the speleological area with the highest concentration of caves in Brazil (and probably in South America). Although more than 300 caves have been examined in this area (Zampaulo 2010), this species was found near the entrances of only two caves, suggesting that they are definitely accidental.

Remarks. Only female samples of *Doru*, which are difficult to identify to the species level, were collected in this study. The external morphologies (Fig. 43) matched those of *D. luteipes* (Scudder 1876; Brindle 1971d; Steinmann 1979; 1993). The females of *D. luteipes* are similar in appearance to *Doru lineare* (Eschscholtz, 1822) [Brindle 1971d; Steinmann 1979, 1993: see also Sakai 1993, 1995 for proposal of a synonymy of this species with *Doru taeniatum* (Dohrn, 1862)]; however, the spermathecal morphologies, including the shape of the spermathecal capsule with seven constrictions (Fig. 44: the spermathecal morphology was examined for the sample from Gruta do Vento cave), were the same as those described by Mariani (1994) for *D. luteipes*. According to Mariani (1994), the spermathecal capsule of *D. lineare* is shorter with fewer and weaker constrictions. This was confirmed in a female sample collected at Varzelândia, Minas Gerais, Brazil on 13.iii.2016 by Y.K., with conspecific males (Fig. 45). However, parthenogenesis has been reported for some Brazilian populations of *D. lineare* (Cocco et al. 2013), suggesting possible polymorphisms in the spermathecal morphology. Thus, the identification of the samples is tentative.

Distribution. Colombia, Surinam, Brazil, Peru, Bolivia, and Argentina.

Discussion

Of the five taxa identified to the species level in this study, *E. brasiliensis* and *D. luteipes* may be accidental inhabitants of caves, while *E. janeirensis* and *P. dorsalis* likely maintain permanent cave populations, but being also found in various non-cave habitats (troglophiles).

At present the association to cave habitats is unknown for *C. cavernicola* sp. n. The species does not present any obvious troglomorphic traits. However, subterranean species do not always possess obvious troglomorphic traits, especially when associated with shallow subterranean habitats. Bartkowiak et al. (1991) compared the eyes of carabids with different degrees of adaptation for cave life, and suggested that troglobites living in superficial subterranean systems are able to use dim light stimuli for orientation using eyes. Some troglobitic carabids that live in shallow subterranean habitats in the Amazon with only partially reduced eyes also support this view (Pellegrini and Ferreira 2011). Accordingly, if *C. cavernicola* sp. n. is mainly associated with shallow subterranean habitats (such as the caves in the type locality) in the extremely dry area with high insolation, it could maintain functional eyes. Further samples and studies on the ecology of this new species are necessary, before determining whether caves are its primary habitat.

The association of Dermaptera with bat guano in caves has been reported for some species around the world: large populations of *Arixenia esau* Jordan, 1909 associated with bat guano piles in Niah caves, Sarawak (Medway 1958), and *Xeniaria* species occurring in high densities in bat guano of caves in the Gunong Mulu National Park (Borneo) (Brindle 1980b). Askew (1971) also reported *Xeniaria jacobsoni* (Burr, 1912) occurring in high densities in bat guano piles in a cave in Java where they prey upon small arthropods. In addition to these Arixeniids, many other species observed in caves were also collected near guano piles (*Irdex chapmani* Brindle, 1980 and *Nala ornata* Borelli, 1932 from caves in Borneo; *Schizochelisoches brevipennis* from caves in Peninsular Malaysia) (Brindle and Oromi 1994), suggesting that guano is an important direct or indirect resource for earwigs in caves. However, except for *E. janeirensis* and *P. dorsalis*, most species found in caves in Brazil seem to be accidental or not directly associated with guano. The reasons for this lack of association remain unknown. Additional studies are necessary to confirm the relations of Brazilian cave-dwelling earwigs to cave environments, as in most cases, only one or two samples were obtained in each cave.

Systematic position of the subfamily Cylindrogastrinae

In the present study, the wing and female genital structures are described for *Cylindrogaster* spp. for the first time. Well-developed ovipositor components [gonoplacs (= coxal lobes) and gonapophyses of the 8th and 9th abdominal segments (gl8, gl9, gp8, and gp9, respectively)] are considered plesiomorphic in Dermaptera (Zacher 1911; Burr 1915a; Hincks 1959; Giles 1963; Klass 2003).

Klass (2003) studied the female genitalia of almost all representative groups of the Protodermaptera (Karschellidae, Haplodiplatyidae, Diplatyidae, and Pygidicranidae *sensu stricto*). Many members of Pygidicranidae *sensu stricto*, including *Echinosoma* (Echinosomatinae), *Dacnodes* (Pygidicraninae), *Tagalina* (Pygidicraninae), and *Anataelia* (Anataelinae), are characterized by a well-developed pair of slender gp8, and a pair of long lobate gl9 that are longer than gl8 and gp9 (Klass 2003). Conversely, the gp8 in the female genitalia of Diplatyinae (*Diplatys*) and Haplodiplatyidae (*Haplodiplatys*) is reduced and usually shorter than gl9 (Klass 2003; Kamimura et al. 2016a). This characteristic is shared with *Karschiella* (Karshiellidae) and *Esphalmenus* (Pygidicranidae *sensu stricto*, Esphalmeninae) (Klass 2003). Thus, the female genitalia of *Cylindrogaster* spp. are of the Diplatyinae − Karshiellidae − *Esphalmenus* type.

Klass (2003) also found a large unpaired gland in nearly all species. A pair of thin, long cuticular tubes (referred to as lateral tubes in Klass 2003) are associated with this gland, which opens on the midline of the body on segment IX. The only exception to this finding was *Diplatys* (Klass 2003). Klass (2003) noted that no similar organs have been recorded in other insect taxa, and thus the lateral tubes are likely autapomorphic for Dermaptera or for a subgroup of them. Lateral tubes have also been reported for *Esphalmenus* (Pygidicranidae) and *Allostethus* (Labiduridae *sensu lato*), which lack the unpaired gland (Klass 2003; Kamimura and Lee 2014b). In this study, we failed to detect an unpaired gland and lateral tubes in the female genital region of *Cylindrogaster* sp. 1 and *Cylindrogaster* sp. 2. Among the members of Protodermaptera, a similar observation was reported for *Diplatys*, in which only a small fold was present immediately behind the base of gonapophyses IX. It was hypothesized that the fold was a vestige of the accessory gland or of the common entrance pouch of the lateral tubes (Klass 2003).

In conclusion, multiple genital and wing traits (see "Remarks" of *Cylindrogaster* sp. 1 and *Cylindrogaster* sp. 2), as well as segmented nymphal cerci, suggested a close relationship between Cylindrogastrinae and Diplatyinae (or Diplatyidae *sensu stricto*). These two groups in the Protodermaptera also had depressed femora with lamelliform edges, an arolium between the claws, and short antennae with fewer than 25 segments (Hincks 1955, 1959; Steinmann 1986). The most notable difference between the two groups is the number of gonopores per virga. However, bifurcated virgae have also been reported in other groups of Pygidicranidae, including the genera *Pyragra*, *Esphalmenus*, and *Cranopygia* (Hincks 1959; Popham 1965a; Brindle 1984).

The subfamily Cylindrogastrinae was originally erected in the family Pygidicranidae (Maccagno 1929). The subfamily was not recognized by Hincks (1955), Popham (1965b, 1969, 1985), Reichardt (1968a) and Günther and Herter (1974) due to its similar external morphology to that of Diplatyinae (Tab. 1). However, Sakai (1971, 1982, 1985, 1996) considered the differences in the virgal morphologies (1 vs. 2 gonopores) important and recognized Cylindrogastrinae and Diplatyinae as distinct subfamilies within Diplatyidae. Steinmann (1975, 1986, 1989b) proposed Diplatyinae and Cylindrogastrinae as subfamilies of the family Pygidicranidae (Tab. 1). Differently, some subsequent studies placed Cylindrogastrinae within Pygidicranidae, while treating Diplatyidae at the family level (Haas and Klass 2003; Engel and Haas 2007). We support the position of Cylindrogastrinae in the Diplatyidae and not in Pygidicranidae (Tab. 1). The subfamily Diplatymorphinae includes only one species, *Diplatymorpha borneensis* Boeseman, 1954, which was described based on a single female specimen in Borneo (Boeseman 1954). According to Steinmann (1986), this subfamily can be separated from the Cylindrogastrinae based on the shape of fifth antennal segment: almost quadrate as the fourth segment in *Diplatymorpha borneensis* whereas visibly longer than the fourth segment in *Cylindrogaster* spp. However, as described for the holotype of *Cylindrogaster cavernicola* sp. n., there may be a considerable variation in the antennal morphology even within an individual. Except for the antennal morphology and slightly sturdier built body, the external morphology of *Diplatymorpha borneensis* resembles those of *Diplatys* species (Boeseman 1954), and therefore multiple researchers treat it as a junior synonym of Diplatyinae (Tab. 1). Accordingly, we tentatively place Diplatymorphinae as a distinct subfamily within Diplatyidae, while Diplatyidae, Haplodiplatyidae, and Pygidicranidae are treated as separate families.

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RESEARCH ARTICLE

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Revision of the West Palaearctic *Polistes* Latreille, with the descriptions of two species – an integrative approach using morphology and DNA barcodes (Hymenoptera, Vespidae)

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Abstract

The genus *Polistes* is revised for the West Palaearctic region based on morphology and DNA barcodes. The revision includes all known West Palaearctic species, raising the number of species in Europe to 14 and to 17 for the West Palaearctic realm. DNA barcodes were recovered from 15 species, 14 of which belong to the subgenus *Polistes*, and one, *P. wattii*, to the subgenus *Gyrostoma*. An integrative taxonomic approach combining morphology and molecular data (DNA barcoding) was employed to resolve longstanding taxonomic problems in this group. Two species, *P. austroccidentalis* van Achterberg & Neumeyer, **sp. n.** (= *P. semenowi* auctt.) from W and SW Europe and *P. maroccanus* Schmid-Egger, **sp. n.** from Morocco are described as new. *Polistes bucharensis* Erichson, 1849, and *P. foederatus* Kohl, 1898, were restored from synonymy. The following new synonyms are proposed: *P. sulcifer* Zimmermann, 1930, and *Pseudopolistes sulcifer* var. *similator* Zirngiebl, 1955, under *P. semenowi* Morawitz, 1889, **syn. n.**; *Polistes iranus* Guiglia, 1976, *Polistes gallica* var. *ornata* Weyrauch, 1938 and *Polistes gallicus muchei* Gusenleitner, 1976, under *P. bucharensis* Erichson, 1849, **syn. n.**; *Polistes omissus* var. *ordubadensis* Zirngiebl, 1955, and *P. hellenicus* Arens, 2011, under *Polistes mongolicus* du Buysson, 1911, **syn. n.** An illustrated key includes all species and additionally three species from the subgenera *Aphanilopterus* Meunier, 1888 and *Gyrostoma* Kirby, 1828 (including a Nearctic species recently introduced to Spain and two species occurring in Egypt, the Arabian Peninsula, and SW Asia). A phylogenetic analysis using Bayesian inference provides insights into phylogenetic relationships within the genus *Polistes*.

Keywords
Taxonomic revision, DNA barcoding, key to species, integrative taxonomy

Introduction

The paper wasp genus *Polistes* Latreille, 1802, is an important model group for behavioural and evolutionary studies (Tibbetts 2007, Hughes et al. 1993, Jandt et al. 2014). It includes many eusocial species that exhibit various forms of social organization. Moreover, the comparatively small colony size of *Polistes* species and their exposed nests facilitate both field observations and experiments (e.g., Cervo et al. 2008). Currently, over 220 species are recognized worldwide (Arens 2011, Buck et al. 2012, Nugroho et al. 2012), 11 of which occur in Europe (Neumeyer et al. 2014, Castro et al. 2013). Three of them, *P. atrimandibularis*, *P. austroccidentalis* sp. n. (= *P. semenowi* auctt.) and *P. semenowi (= P. sulcifer* Zimmermann, 1930), are social parasites (Cervo 2006, and references therein) and were formerly placed in a separate genus (or subgenus) *Sulcopolistes* Blüthgen, 1938 (Blüthgen 1961, Guiglia 1972) until Carpenter (1990) synonymized *Sulcopolistes* with *Polistes*. Subsequently, a phylogenetic analysis showed that the three socially parasitic species form the sister clade to a clade consisting of *P. dominula* (Christ, 1791) and *P. nimpha* (Christ, 1791) and that this clade is nested within the European *Polistes* species (Choudhary et al. 1994).

Blüthgen (1943) proposed the subgeneric name *Leptopolistes* for several non-parasitic European species, including the type species *P. associus* (Kohl, 1898) (Table 2). Males of these taxa share immediately narrowing temples (genae) in dorsal view (Blüthgen 1943, Guiglia 1972), giving the male head a characteristic shape. Currently, all European *Polistes* species are assigned to the subgenus *Polistes* (Carpenter 1996), although the species formerly included in *Leptopolistes* were still considered to be closely related (Carpenter 1997). In the present study, we are using "*P. gallicus* species group" to refer to the former subgenus *Leptopolistes*, and "*P. dominula* species group" for the remaining species, albeit with some changes from the traditional view (see Table 2).

The taxonomy of the *P. gallicus* species group has been notoriously difficult (see, for example Guiglia 1972, Arens 2011, Neumeyer et al. 2014, 2015). In the present study, an attempt was made to clarify the taxonomic status of all *Polistes* species of the West Palaearctic region, including a list of all available names of the genus, and to provide a key to species. Also, new names are proposed for two social parasitic species from NW Africa and SW Europe, one of them (*P. maroccanus* Schmid-Egger, sp. n.) new to science. Two other species (*P. bucharensis* Erichson, 1849, and *P. foederatus* Kohl, 1898) were restored from synonymy, thus raising the number of valid species in Europe to 14, and to 17 for the West Palaearctic region. Additionally, three species from other subgenera (an American species recently introduced into Spain and two southern species occurring in Egypt, Arabian Peninsula, and SW Asia) are included in the key.

The present study employs the concept of integrative taxonomy (Schlick-Steiner et al. 2010) and compares results from morphological examinations with results from DNA barcoding (see Schmidt et al. 2015 for further details). The morphological data are supplemented with published data (Neumeyer et al. 2014, 2015) and unpublished sources, the latter kindly provided from Aleksandar Ćetković (Belgrade) to Kees van Achterberg.

Materials and methods

Sampling

Specimens for DNA barcoding are primarily deposited in the collections of the Zoologische Staatssammlung München and the private collection of CSE. 264 specimens representing all West Palaearctic species of the subgenus *Polistes* and the subgenus *Gyrostoma* were processed, the latter being represented by the single species *P. wattii* Cameron, 1900. For DNA extraction, a single leg was removed from each specimen (for further details see Schmidt et al. 2015).

For the present study, a large number of specimens from several collections were morphologically examined. The taxonomic treatment of species is primarily based on the combined analysis of morphological and molecular data, and only those specimens that were analysed both, morphologically and genetically, are listed in the Suppl. material 1.

DNA extraction and PCR

DNA extraction, PCR amplification, and sequencing were conducted at the Canadian Centre for DNA Barcoding (CCDB) using standardised high-throughput protocols (Ivanova et al. 2006, de Waard et al. 2008), available online under www.ccdb.ca/resources. The 658bp target region, starting from the 5' end of the mitochondrial cytochrome oxidase *c* (COI) gene, includes the DNA barcode region of the animal kingdom (Hebert et al. 2003). The DNA extracts are stored at the CCDB with aliquots being deposited at the "DNA Storage" facility at the ZSM (see www.zsm.mwn.de/einrichtungen/dna-storage/?lang=en). Specimens that were successfully sequenced are listed under Supporting Information, with sequence lengths and the number of unresolved bases. Detailed specimen and sequence data are accessible in BOLD as a single citable dataset (dx.doi.org/10.5883/DS-WPPOLIST). The sequences are also available on GenBank (for accession numbers see Suppl. material 1).

Molecular analyses

Sequence divergence statistics were calculated using the Kimura two-parameter model of sequence evolution (Kimura 1980). Sequences shorter than 500bp were excluded from the distance calculations and the phylogenetic analysis. The BIN is assigned by the BOLD system and represents a globally unique identifier for a cluster of sequences that has shown to correspond closely to a biological species (Ratnasingham & Hebert 2013), including Hymenoptera (Schmidt et al. 2015, 2016) and other insects (Hausmann et al. 2011, Raupach et al. 2014, Hendrich et al. 2015, Mutanen et al. 2016). Genetic distances and summary indices were calculated using analytical tools in BOLD and are given as mean and maximum pairwise distances for intraspecific variation, and as minimum pairwise distances for interspecific variation (see Table 1).

Phylogenetic analysis

The COI sequence data were submitted to a phylogenetic analysis using MrBayes version 3.2 (Ronquist and Huelsenbeck 2003) after alignment using the BOLD Aligner. Duplicates of identical sequences were removed from the dataset so that each haplotype was represented by a single sequence. The analysis employed separate, unlinked substitution models for codon positions of the COI sequence fragment. Two independent runs with one cold and three heated chains were run for five million generations after which the average standard deviation of split frequencies reached values lower than 0.01. The resulting tree was rooted using two basal outgroup taxa (Peters et al. 2017), including one representative of the Eumeninae (*Eumenes pedunculatus*) and one species of Masarinae (*Celonites abbreviatus* (Villers)).

Acronyms of depositories and other institutions

CSCF	Centre Suisse de Cartographie de la Faune, Neuchâtel, Switzerland
CSE	Christian Schmid-Egger, Berlin, Germany
CvA	Kees van Achterberg, Leiden, The Netherlands
ETHZ	Entomologische Sammlung der Eidgenössischen Technischen Hochschule Zürich, Switzerland
HNHM	Hungarian Natural History Museum, Budapest, Hungary
LSL	Linnean Society of London, London, United Kingdom
MFNB	Museum für Naturkunde, Berlin, Germany
MNHN	Muséum national d'Histoire naturelle, Paris, France
MSNG	Museo di storia naturale Giacomo Doria, Genova, Italy
MSNM	Museo civico di storia naturale, Milano, Italy
MSNV	Museo di Storia Naturale di Venezia, Italy
MZL	Musée cantonal de zoologie, Lausanne, Switzerland

Table 1. Barcoding statistics of *Polistes* species with distribution, Barcode Index Number (BIN), number of specimens (n), mean intraspecific distance, maximum intraspecific distance, nearest neighbour species, and distance to nearest neighbour species. Distances are based on the Kimura 2P model, country codes follow ISO 3166-1.

***Polistes* species**	**BIN**	**n**	**Country**	**Mean intraspecific distance**	**Maximum intraspecific distance**	**Nearest *Polistes* species**	**Distance to NN**
P. albellus	BOLD:AAN3553	12	CH, DE, KZ	0.03	0.16	*P. bischoffi*	2.31
P. associus	BOLD:ACG2253	7	HR, IT	0	0	*P. nimpha*	4.82
P. atrimandibularis	BOLD:AAN4297	2	IT	0	0	*P. semenowi*	1.7
P. austroccidentalis	BOLD:ACG1677	5	CH, FR, MA	0.58	0.95	*P. atrimandibularis*	2.18
P. biglumis	BOLD:AAN3552	21	DE, IT	0.57	1.17	*P. bischoffi*	2.48
P. bischoffi	BOLD:ACG2292	11	CH, FR, HR, SP	0.14	0.32	*P. albellus*	2.31
P. bucharensis	BOLD:ACM7975	9	AZ, CY	1.03	2.03	*P. dominula*	3.29
	BOLD:ACR2719	1	AZ				
	BOLD:ACY7463	3	GR				
P. dominula	BOLD:AAA9495	14	DE, FR	2.45	5.42	*P. bucharensis*	3.29
	BOLD:AAB7105	37	AZ, CH, DE, GR, HR, IT				
	BOLD:ACR3974	10	MA				
P. foederatus	BOLD:ACG2291	21	AZ, GR, HR, IT, TR	0.49	1.29	*P. biglumis*	2.88
P. gallicus	BOLD:AAN3302	20	HR, IT, PT, SP	0.28	1.09	*P. biglumis*	2.49
	NONE	2	AZ, DE				
P. maroccanus	BOLD:ACR4397	1	MA	N/A	0	*P. atrimandibularis*	3.78
P. mongolicus	BOLD:AAN3303	51	AZ, CY, GR, HR, IT, TR	0.88	2.04	*P. biglumis*	2.99
P. nimpha	BOLD:AAL0103	18	DE, GR, IT	2.2	6.28	*P. dominula*	3.56
	BOLD:ACC1661	4	DE				
P. semenowi	BOLD:ACG1290	6	CH, IT	0.28	0.65	*P. atrimandibularis*	1.7
P. wattii	BOLD:AAE1384	4	UAE	0	0	*P. gallicus*	12.84

NHMW	Naturhistorisches Museum Wien, Austria
NMBE	Naturhistorisches Museum der Burgergemeinde Bern, Switzerland
OLL	Oberösterreichisches Landesmuseum Linz, Austria.
RMNH	Naturalis Biodiversity Center, Leiden, the Netherlands
RN	Rainer Neumeyer, Zürich, Switzerland
ZISP	Zoological Institute of the Russian Academy of Sciences, St Petersburg, Russia
ZSM	Zoologische Staatssammlung München, Munich, Germany
ZMUZ	Zoologisches Museum der Universität Zürich, Switzerland

Abbreviation used in the key and descriptions

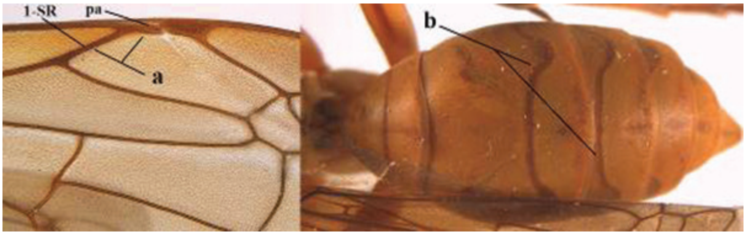
POL	Postocellar diameter, the distance between the lateral ocelli.

Results

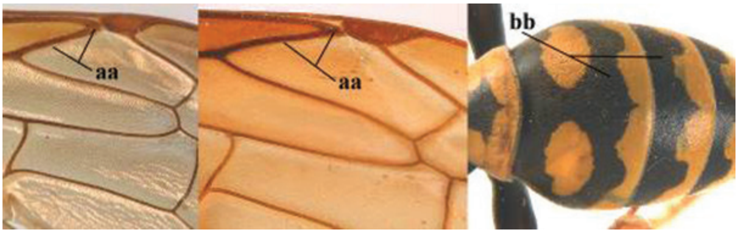
Key to West Palaearctic species of the genus *Polistes* Latreille

Regional terms of geographic distribution are abbreviated as Central (C), Southern (S), Eastern (E), Northern (N) and West (W). Southwest Asia includes Turkey, Iran, Israel and adjacent countries. Temperate Asia refers to Asia north of 37° northern latitude (approximative only, species may occur south of 37° north, e.g. in mountain regions).

1 Parastigma elongate and long compared to length of vein 1-SR of fore wing (a); second and third metasomal tergites with brown or blackish curved lines (b); [mesopleuron only sparsely punctate medially]; subgenus *Gyrostoma*.... **2**

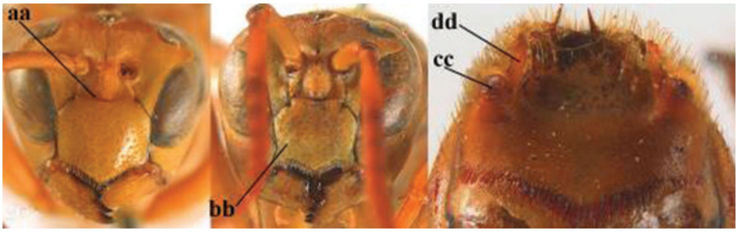


– Parastigma short, hardly or not longer than wide and short compared to length of vein 1-SR of fore wing (aa); second and third metasomal tergites without curved lines, often with a black pattern (bb) **3**

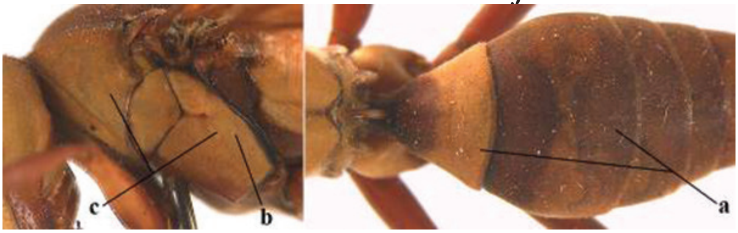


2 Female: Dorsal part of epistomal (frontoclypeal) suture blackish or dark brown (a); length of fore wing 15–28 mm. Male: Clypeus evenly convex (b); lateral tubercles on each side of apex of last sternite subtriangular and wider basally (c), its terminal apophyses long and spatulate apically (d); Palaearctic distribution: Egypt, Oman, Iran, Afghanistan .. ***P. olivaceus*** **(DeGeer, 1773)**

– Female: Dorsal part of epistomal suture yellowish (aa); length of fore wing 11–17 mm. Male: Clypeus with impression (bb); lateral tubercles of last sternite more cylindrical and narrower basally (cc), its terminal apophyses long and pointed apically (dd); Palaearctic distribution: Afghanistan, Iran, Iraq, Saudi Arabia, United Arab Emirates, Oman, China...........***P. wattii*** **Cameron, 1900**

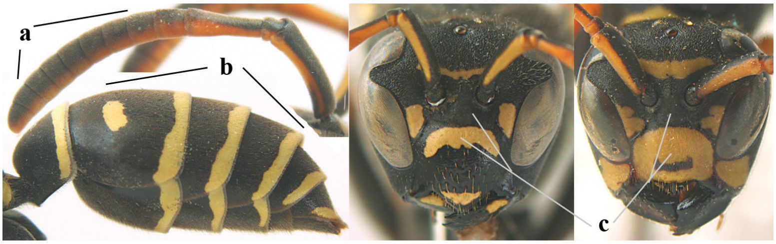


3 Body brown with yellow pattern (a); mesopleuron indistinctly sculptured (b, c); recently introduced to northern Spain, native to South and Central America, Caribbean islands and southern U.S.A. (subgenus *Aphanilopterus*)................... .... ***P. major*** **Palisot de Beauvois, 1818**

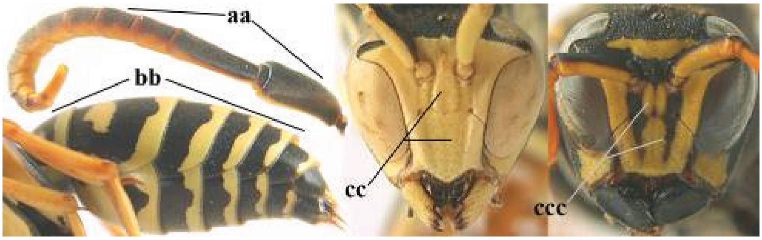


– Body black with yellow pattern (aa); mesopleuron with dense irregular microstriae (bb, cc) (subgenus *Polistes*) **4**

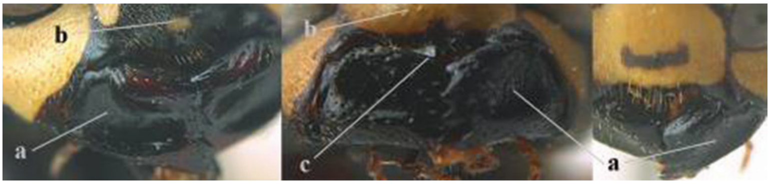
4 Antenna with 12 segments (a); metasoma with 6 visible tergites and sternites (b); face and/or clypeus with yellow and black pattern (c); females **5**



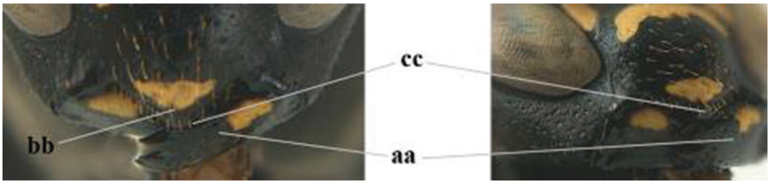
– Antenna with 13 segments (aa); metasoma with 7 visible tergites and sternites (bb); face and/or clypeus yellow (cc; but more or less blackish pattern present in *P. atrimandibularis* ccc); males **21**



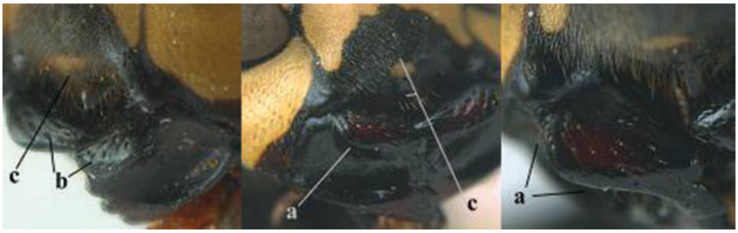
5 Mandible very stout and its outer face more or less depressed (a); ventral border of clypeus strongly convex (b) and medially acute (c); socio-parasitic species... **6**



– Mandible comparatively slender and its outer face weakly convex or flat (aa); ventral border of clypeus flat (bb) and medially truncate or slightly concave (cc); social species **9**

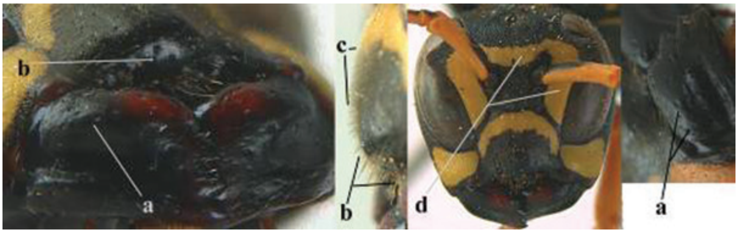


6 Basal half of mandible distinctly angulate (a) and flattened (b); clypeus gradually depressed ventrally (c); [yellow area along inner eye margin connected to yellow bar above antennal sockets; clypeus largely punctate ventrally and with fine pubescence as in medial area (c)]; SE and southern C Europe, C Asia [= *P. sulcifer* Zimmermann, 1930] ....***P. semenowi*** **Morawitz, 1889**

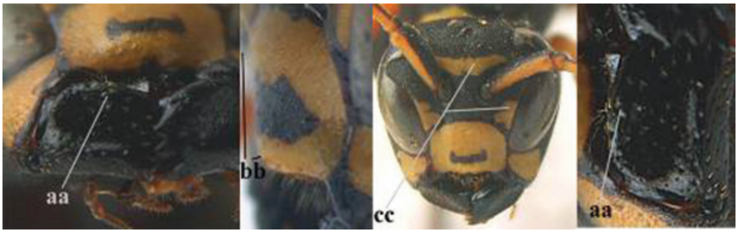


– Basal half of mandible gradually curved (aa) and convex (bb); clypeus abruptly depressed ventrally (cc) **7**

7 Dorsal ridge of mandible wide, convex and distinctly elevated above middle of mandible (a, b); fine pubescence of clypeus conspicuous and comparatively long (b, c); yellow area along inner eye margin usually connected with yellow bar above antennal sockets (d); SW and southern C Europe, N Africa; [= *P. semenowi* auctt.] ...***P. austroccidentalis*** **van Achterberg & Neumeyer, sp. n.**

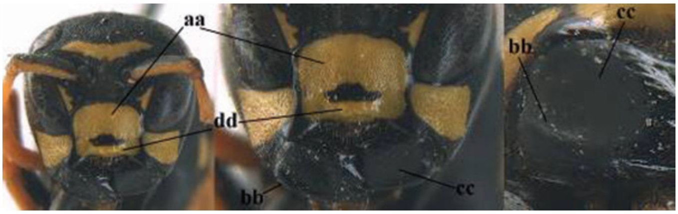


– Dorsal ridge of mandible narrow, slightly convex and hardly elevated above middle of mandible (aa); fine pubescence of clypeus inconspicuous and short (bb); yellow area along inner eye margin separated from yellow bar above antennal sockets (cc) **8**

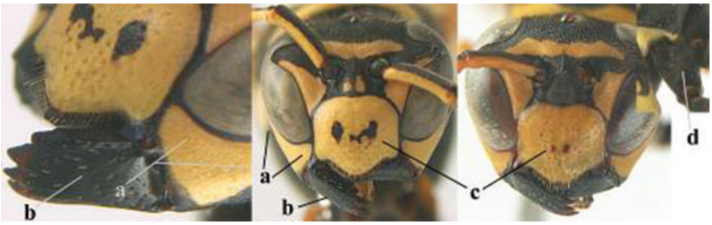


8 Clypeus 0.7 times as long as wide (a); lower ridge of mandible 0.4 times as wide as mandible (b); depression of mandible with rather dull surface (c); area above lower edge of clypeus (below dark spot) dull and straight (d); S and southern C Europe to W Asia ..... ***P. atrimandibularis* Zimmermann, 1930**

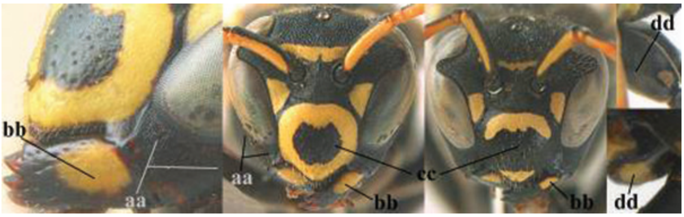
– Clypeus 0.8–0.9 times as long as wide (aa); lower ridge of mandible 0.2 times as wide as mandible (bb); depression of mandible with shiny surface (cc); area above lower edge of clypeus (below dark spot) shiny and distinctly convex (dd); Morocco .... ***P. maroccanus* Schmid-Egger, sp. n.**



9 Malar space mainly yellow and connected to yellow ventral part of temple (a); mandible usually black (b), **if** mandible with yellow patch then total yellow area smaller than yellow area of malar space and temple; clypeus somewhat wider than high medially (c); hind coxa black dorsally (d); *dominula*-group **10**



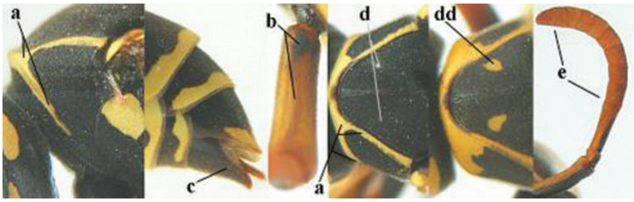
– Malar space black as ventral part of temple (aa); **if** rarely with small yellow patch then total yellow area of mandible larger than that of yellow patch of malar space and usually not connected to ventral yellow part of temple; mandible with yellow patch (bb); clypeus about as wide as high medially (cc); dorsal colour of hind coxa variable (dd, d); *gallicus*-group **16**



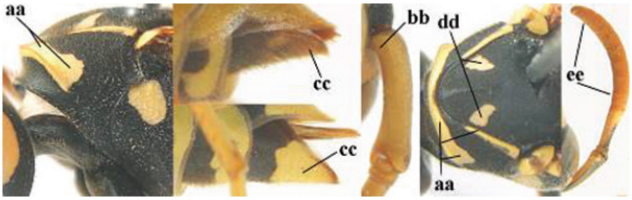
10 Specimens from Europe (excluding Crete) and NW Africa **11**

– Specimens from Asia (including Crete and Cyprus) **13**

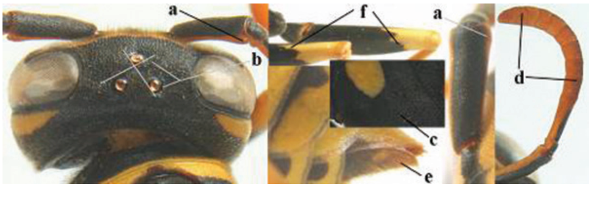
11 Transverse yellow band of pronotum narrower medio-laterally than dorso-laterally near junction with oblique yellow stripes of pronotum (a), rarely narrowed dorso-laterally and slightly widened below it **and then** mesoscutum usually without yellow markings (d); scapus more or less dark brown or blackish baso-ventrally (b), apical half of hypopygium often entirely black or dark brown (c), sometimes with small yellow spot, rarely apical quarter of hypopygium yellow; mesoscutum usually without paired yellow spots (d) but sometimes minute, or medium-sized (dd); apical half of antenna more or less darkened dorsally (e); Europe and Palaearctic Asia .... ***P. nimpha*** **(Christ, 1791)**



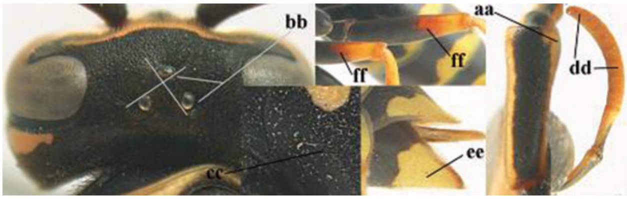
– Transverse yellow band of pronotum as wide medio-laterally as dorsolaterally or wider (aa; rarely narrowed medio-laterally and slightly widened below it) **and** mesoscutum usually with two yellow spots (dd); scapus entirely yellow baso-ventrally (bb), rarely slightly infuscate; colour of apical half of hypopygium variable, often entirely yellow or apically brownish (cc), rarely entirely black; mesoscutum with paired yellow spots usually medium-sized to large (dd), rarely minute or absent; apical half of antenna evenly orange or yellow dorsally (ee), but more or less infuscate in *P. associus* **12**



12 Scapus slightly widened apically in dorsal view (a), if scapus intermediate then ocellar triangle acute anteriorly (b); change in sculpture between mesepisternum and epicnemium frequently gradual (c; = epicnemial ridge indistinct); apical half of antenna more or less brownish dorsally (d); apical half of hypopygium (= sternite VI) often largely black and brown or largely brown, slightly darker than apex of last tergite (e); border of black and yellow on outer side of middle and hind femora often sharp and often without orange intermediate area in Balkan populations (f); often smaller species; S Europe, W Asia ***P. associus*** **Kohl, 1898**

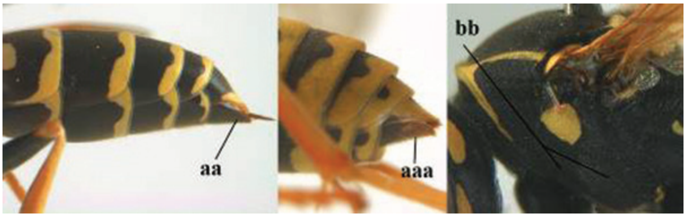


– Scapus distinctly widened apically in dorsal view (aa); ocellar triangle transverse (bb); change in sculpture between mesepisternum and epicnemium abrupt (cc; = epicnemial ridge distinct); apical half of antenna orange or yellow (dd); apical half of hypopygium yellow or largely so and as pale as apex of apical tergite (ee), rarely darker; border of black and yellow on outer side of middle and hind femora washed out, partly because of orange intermediate area (ff); somewhat larger species); Europe except N, NW Africa, W and C Turkey, Azerbaijan, probably also farther east in temperate Asia. Not in Crete, see *P. bucharensis* (couplet 14) .... ***P. dominula*** **(Christ, 1791)**



13 Apical half of sternite VI yellow or largely so, and as yellow as apex of last tergite (a); ventral part of mesopleuron in general more coarsely sculptured than remaining parts (b); [mesoscutum usually with two yellow spots; apical half of antenna orange or yellow reddish].. **14**

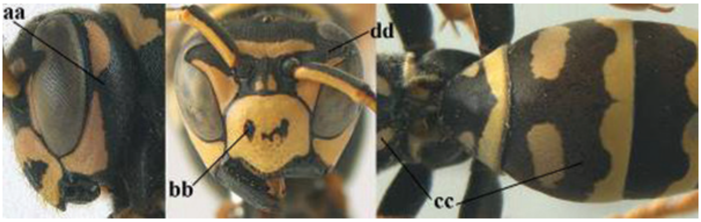
– Apical half of sternite VI largely black, **if** with reddish or yellowish apical part then pale part smaller than black part of tergite VI (aa), but especially in *P. associus* sometimes paler and not obviously smaller than black part of last tergite (aaa); mesopleuron ventrally evenly and finer sculptured (bb) **15**



14 Temple (gena) with wide yellow band, medially wider than half width of temple (a); clypeus yellow medially (b); propodeum and second tergite largely yellow (c); incision of eye mainly yellow (d); [frons slightly convex (about similar to area between antennal sockets and distinctly less so in *P. dominula*) and mainly yellow, extent of yellow area variable, sometimes reaching ocellar

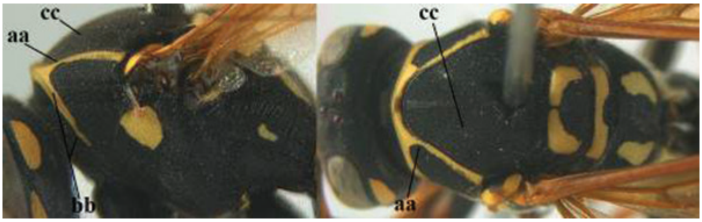
area, scapus often largely yellow dorsally]; W and C Asia, Cyprus, Egypt, Crete (specimens from Crete differ in colour pattern, see description below)...........
....***P. bucharensis* Erichson, 1849**

– Temple with separated yellow spots (aa), **if** connected then band medially narrower than half width of temple; clypeus with medial black spot, may lack in few specimens (bb); propodeum and second tergite largely black (cc); incision of eye mainly black (dd); [bristles of clypeus conspicuous]; W and C Turkey, Azerbaijan, probably also farther east in temperate Asia....................
....***P. dominula* (Christ, 1791)**

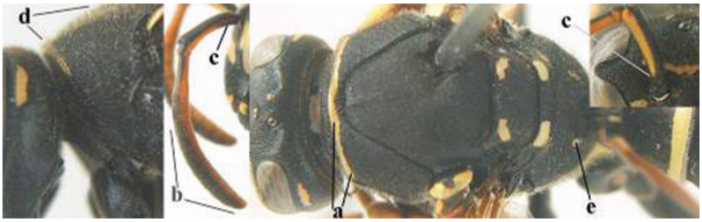


15 Posterolateral yellow bands of pronotum usually not connected to anterior transverse band (a); anterior transverse yellow band of pronotum medio-laterally as wide as dorso-laterally or wider (b); mesoscutum with paired yellow spots (c); [clypeus with transverse black band; hypopygium all black, with apical yellow or reddish spot or entirely reddish; distinction from *P. nimpha* in SW Asia is not always possible, because *P. nimpha* is highly variable in this region; usually sculpture of ventral part of mesopleuron finer in *P. associus* than in *P. nimpha*]; southern Europe, western Asia....***P. associus* Kohl, 1898**

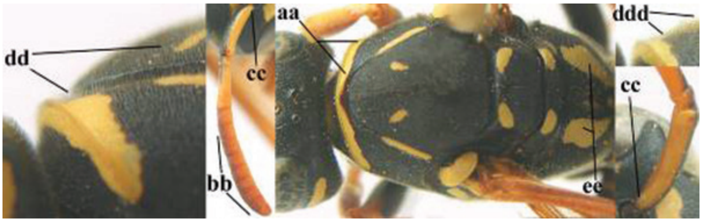
– Posterolateral yellow bands of pronotum usually connected to anterior transverse band (aa); anterior transverse yellow band of pronotum medio-laterally narrower than dorso-laterally (bb); mesoscutum sometimes lacking yellow spots (cc); [colour pattern is highly variable in this species, more so than in Europe]; Europe and Palaearctic Asia .... ***P. nimpha*** **(Christ, 1791)**



16 Transverse yellow band of pronotum narrow (a); antenna largely black or blackish dorsally (b), similar to colour of frons; basal third of scapus more or less black or blackish ventrally (c); pubescence of pronotum and mesoscutum 0.7–0.9 times as long as diameter of anterior ocellus (d); yellow spots of propodeum narrow or absent, **if** present then usually narrower than minimum distance between spots (e); [malar space at least 0.87 times as long as POL] **17**



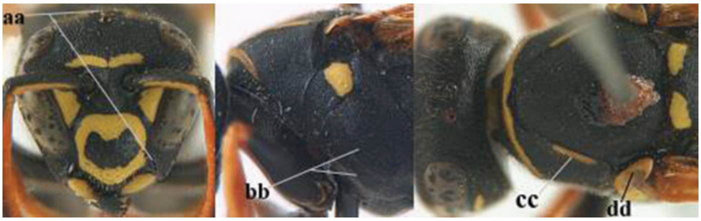
\- Transverse yellow band of pronotum wider (aa); antenna orange brown or somewhat darkened dorsally (bb) and distinctly paler than frons; basal third of scapus yellow ventrally (cc), but darkened in most *P. foederatus*; pubescence of pronotum and mesoscutum about half as long as diameter of anterior ocellus (dd), but longer in *P. bischoffi* (ddd); yellow spots of propodeum wide and usually larger (ee), but sometimes smaller in *P. foederatus*; [malar space usually shorter than 0.87 times POL, except in *P. foederatus*] **18**



17 Malar space 1.22–1.76 times as long as POL (a); change in sculpture and level between mesepisternum and epicnemium abrupt (b; = epicnemial ridge distinct); yellow lateral stripes of pronotum usually absent (c); tegula in most specimens with large dark medial spot, reaching outer margin (d); pubes-

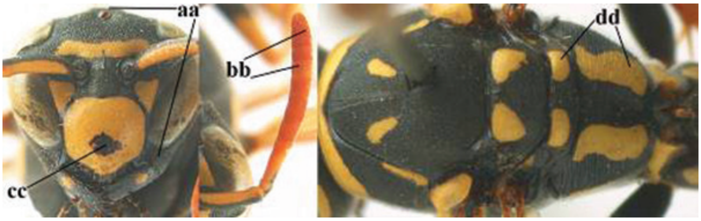
cence of mesoscutum on average 0.9 times as long as greatest diameter of anterior ocellus; Europe, temperate Asia .... ***P. biglumis*** **(Linnaeus, 1758)**

– Malar space 0.87–1.19 times as long as POL (aa); change in sculpture and level between mesepisternum and epicnemium often gradual (bb; = epicnemial ridge absent or obsolescent); yellow lateral stripes of pronotum present (cc; but absent in Mongolian specimens); tegula in most specimens entirely yellow, at most blackish subbasally (dd); pubescence of mesoscutum on average 0.7 times as long as greatest diameter of anterior ocellus; C Europe, temperate Asia ....***P. albellus*** **Giordani Soika, 1976**

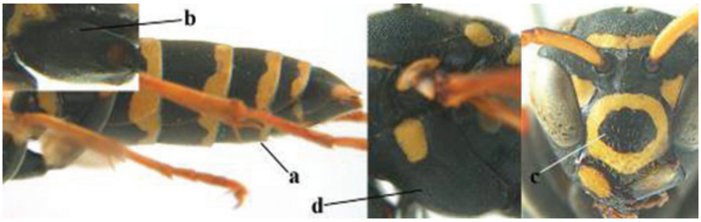


18 Malar space 0.85–1.0 times as long as POL (a); distal half of antenna slightly darker dorsally (b); clypeus with central black patch, may lack in few specimens (c); metanotal and propodeal spots as in (d) [yellow dorsal spot of hind coxa large to absent; hind tibia dorsally with dark brown patch and at both, inner and outer side often with small preapical brown spot; yellow bands of sternites IV-V often medially interrupted; distinct difference in sculpture between mesepisternum and epicnemium (= epicnemial ridge distinct)]; N Italy to SE Europe, Turkey and Central Asia... ***P. foederatus*** **Kohl, 1898**

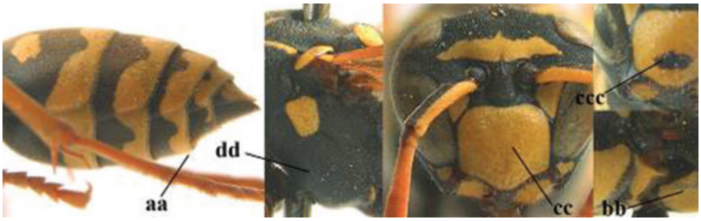
– Malar space at most 0.75 times as long as POL (aa); antenna as pale dorsally as ventrally (bb), but darker dorsally in some *P. bischoffi*; central dark patch on clypeus usually smaller and situated below middle of clypeus or absent (cc; except in *P. bischoffi*); propodeal and metanotal spots according to picture (dd) **19**



19 Apical yellow band of sternite IV medially interrupted (a) or narrow; hind coxa black dorsally (b); clypeus often with a wide black transverse band or with more or less transverse trapezoid black patch, often close to or connected with lateral margins of clypeus and situated nearly halfway clypeus (c); change in sculpture between mesepisternum and epicnemium frequently gradual (d; = epicnemial ridge indistinct); southern C and S Europe............. .... ***P. bischoffi*** **Weyrauch, 1937**

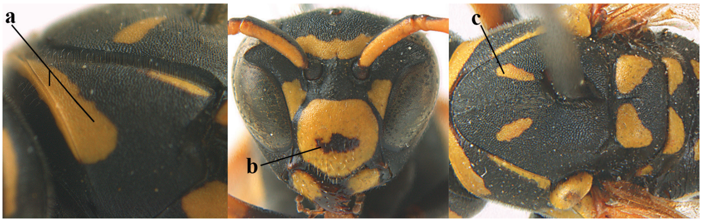


– Apical yellow band of sternite IV usually complete and wide (aa); hind coxa with yellow patch dorsally (bb); central dark patch on clypeus usually less developed and situated below middle of clypeus (ccc) or absent (cc); usually with an abrupt change in sculpture between mesepisternum and epicnemium (dd; = epicnemial ridge distinct), but sometimes rather gradual **20**

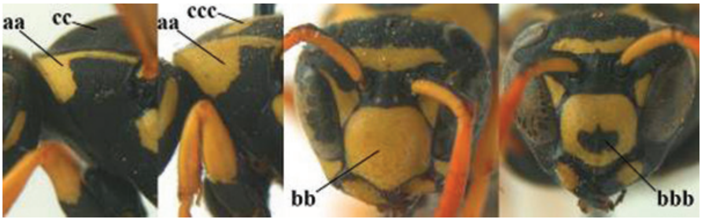


20 Transverse yellow band of pronotum medio-laterally wider than dorso-laterally (a); central dark patch on clypeus usually developed, but small, rounded or forming a transverse band (b); mesoscutum usually with pair of medium-sized to large yellow spots (c); [some specimens have an all yellow clypeal disk and all black mesoscutum; specimens from NW Africa often have sternite IV apically yellow, which is more or less darkened in northern specimens]; NW

Africa, SW Europe, N Italy, southern Switzerland, Croatia, Corfu................ .... ***P. gallicus* (Linnaeus, 1767)**

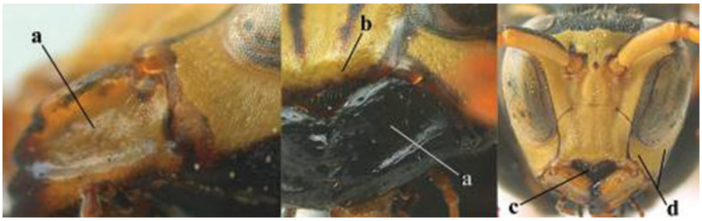


– Transverse yellow band of pronotum dorso-laterally wider than medio-laterally (aa); clypeus entirely yellow (bb) or with minute black spot, but spot sometimes medium-sized (bbb); mesoscutum usually black (cc) or with pair of small yellow spots (but sometimes large in Asian specimens; ccc); Croatia and SE Europe, Turkey, Cyprus to Central Asia and Egypt .... ***P. mongolicus* du Buysson, 1911, stat. rev.**

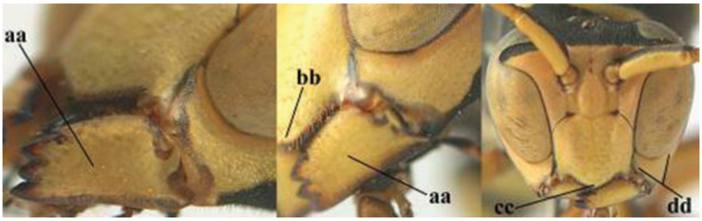


Males

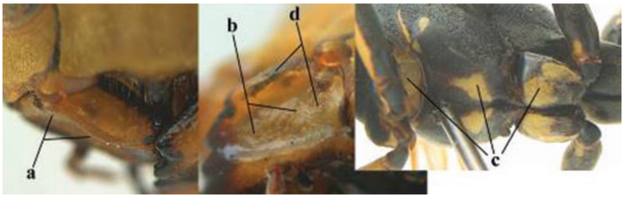
21 Mandible very stout and with a distinct depression on its outer face (a); clypeus depressed medio-apically (b), its margin tapered to a small point (c); malar space comparatively long and wide (d); socio-parasitic species...................... **22**



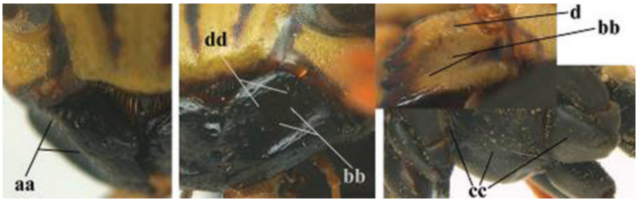
– Mandible comparatively slender and its outer face flat or slightly convex (aa); clypeus flat medio-ventrally (bb), its margin evenly convex or broadly triangular (cc); malar space medium-sized (dd) or narrow; social species **24**



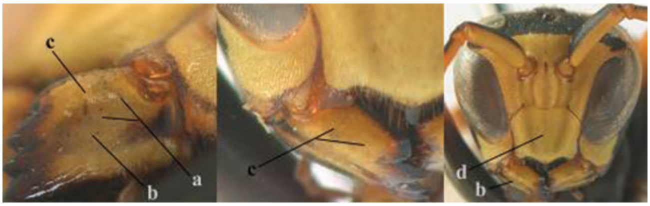
22 Basal half of mandible sinuate in dorsal view (a); mandibular depression strongly concave (b); [mandible mainly yellow or brown (d); fore and middle coxae and mesopleuron ventrally usually with yellow pattern (c); dorsal ridge of mandible at most 0.25 times mandibular width and prominent]; SE and southern C Europe to Central Asia ....***P. semenowi*** **Morawitz, 1889**



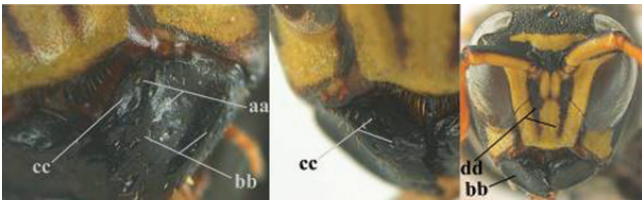
– Basal half of mandible straight in dorsal view or nearly so (aa); mandibular depression shallowly concave (bb); [fore and middle coxae and mesopleuron ventrally usually black (cc), colour of mandible variable (d, dd)]...............**23**



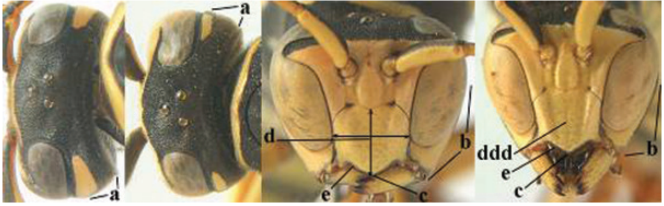
23 Mandible mainly yellow, except for its more or less darkened margins (a); mandibular depression shorter and occupying less than half of outer face of mandible (b), dorsal ridge at least 0.33 times as wide as mandible (c); clypeus entirely yellow medially (d); SW Europe, southern C Europe, NW Africa.... ....***P. austroccidentalis*** **van Achterberg & Neumeyer, sp. n.**



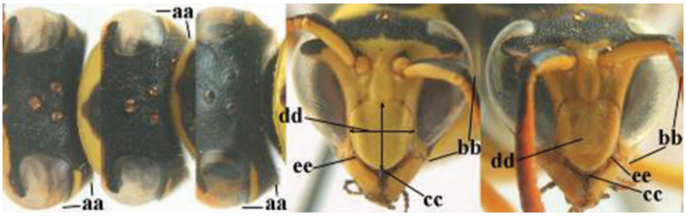
– Mandible black (aa), rarely with small yellow spot; mandibular depression wide and occupying most of outer face of mandible (bb), dorsal ridge 0.25–0.30 times mandibular width (cc); clypeus medially with dark brown pattern (dd), but sometimes largely reduced or absent; S Europe and southern C Europe to W Asia. [If from Morocco consider *P. maroccanus* (male unknown)]................ .... ***P. atrimandibularis*** **Zimmermann, 1930**



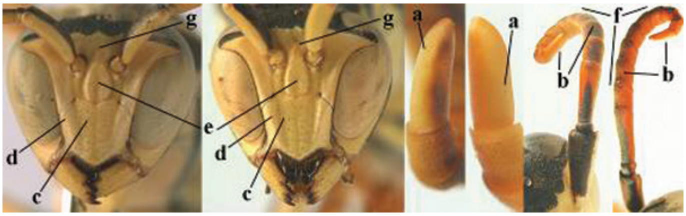
24 Temple bulged behind eye in dorsal view, slightly convex (a); head trapezoid in anterior view (b); apical margin of clypeus triangular (c); width of clypeus 1.0–1.1 times its length (d, ddd); latero-ventral margin of clypeus narrowly black or dark brown and convex in lateral view (e), but flattened in *P. biglumis*........... **25**



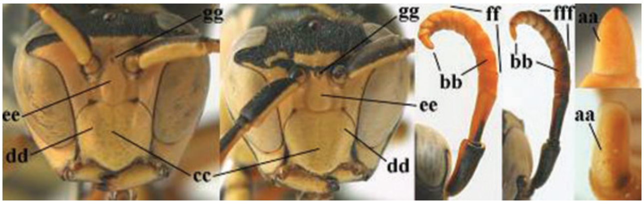
– Temple narrowed behind eye in dorsal view, more or less straight (aa); head nearly triangular in anterior view (bb), but less so in *P. bischoffi*; apical margin of clypeus rounded (cc) or subtruncate; width of clypeus 0.9–1.1 times its length (dd); latero-ventral margin of clypeus yellow and flattened (ee)...... **28**



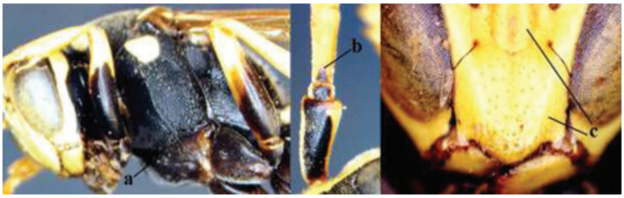
25 Dorsal length of apical antennal segment 2.2–2.9 times as long as its maximal width (a), 1.3–1.5 times as long as fifth antennal segment (b); clypeus distinctly depressed medially (c) and with distinct lateral ridges (d); medio-longitudinal depression of face more or less impressed and U-shaped (e); antenna coloured according to fig. f; short carina between antennal sockets sharp dorsally and usually pale yellow (g); clypeus with short bristles and medio-ventrally flat; width of clypeus 1.0–1.1 times its length; [head sometimes distinctly narrowed ventrally]; Europe and Palaearctic Asia.................
.... ***P. nimpha* (Christ, 1791)**



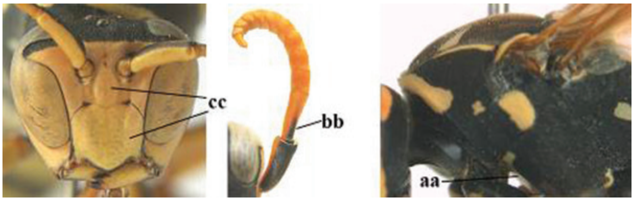
– Dorsal length of apical antennal segment 1.5–2.1 times as long as its maximal width (aa), 1.0–1.2 times as long as length of fifth antennal segment (bb); clypeus not or slightly depressed medially (cc) and lateral ridges absent dorsally or slightly developed (dd); face flat medially, without longitudinal depression (ee); antenna coloured as in ff or fff; short carina between antennal sockets obtuse dorsally and more or less infuscate (gg); width of clypeus 1.1–1.2 times its length.. **26**



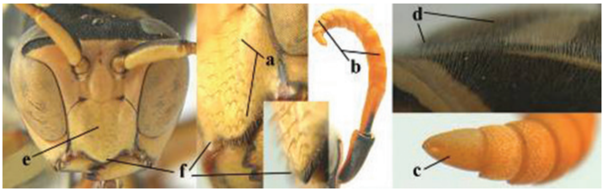
26 Mesosternum entirely black (a); black baso-dorsal stripe on third antennal segment 0.25 times length of segment (b); lateral ridges of clypeus and ridge between antennal socket and clypeus more distinct (c); [largely yellow coloured species, specimens from eastern Turkey however may have reduced whitish yellow markings; W and C Asia, Cyprus, Egypt, Crete.......... ***P. bucharensis*** **Erichson, 1849**



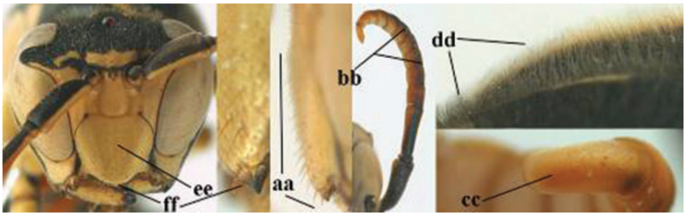
– Mesosternum at least with some yellow spots posteriorly (aa), and often entirely yellow, but in some males of *P. dominula* from southern Greece entirely black; black baso-dorsal stripe on third antennal segment at least 0.5 times length of segment (bb); clypeus laterally nearly flat and ridge between antennal socket and clypeus indistinct (cc) **27**



27 Most of clypeus with long bristles and distinct punctures (a); apical half of antenna uniformly orange-yellow dorsally and ventrally (b); apical antennal segment comparatively stout and dorsally about 1.5 times as long as wide basally (c); setae of pronotum medio-dorsally and of mesoscutum about half as long as width of posterior ocellus (d); width of clypeus 1.1 times its length (e) and medio-ventrally more flattened (f); [fourth and fifth antennal segments strongly oblique in lateral view]; Europe (for specimens from Crete see also *P. bucharensis*), NW Africa, W and C Turkey, Azerbaijan, probably more eastern in temperate Asia.... ***P. dominula*** **(Christ, 1791)**

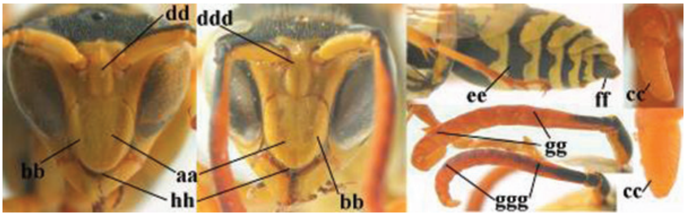


– Dorsal 0.7 of clypeus without bristles and punctures (aa); apical half of antenna usually darker dorsally than ventrally (bb); apical antennal segment more slender, dorsally about twice as long as wide basally (cc); setae of pronotum mediodorsally and of mesoscutum at least 0.8 times as long as width of posterior ocellus (dd) or longer; width of clypeus about equal to its length (ee) and medio-ventrally less flattened (ff); [fourth and fifth antennal segments moderately oblique in lateral view]; Europe, temperate Asia .... ***P. biglumis*** **(Linnaeus, 1758)**

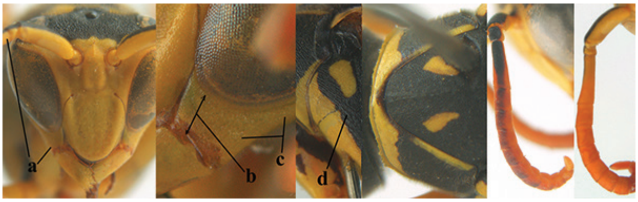


28 Ventral half of clypeus distinctly depressed (a) and with distinct lateral ridges (b); dorsal length of apical antennal segment about 3.0 times its width (c); frons with a distinct longitudinal depression medially (d); sternites III-VII usually with transverse yellow band basally (e; visible with sternites sufficiently extruded) and last sternite often partly yellow (f); apical half of antenna usually distinctly darkened dorsally (g); clypeus more or less truncate medioventrally (h); S Europe, W Asia .... ***P. associus*** **Kohl, 1898**

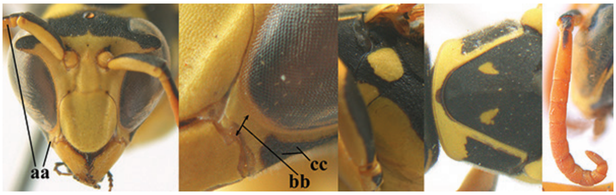
– Ventral half of clypeus at most slightly depressed (aa) but without lateral ridges (bb); dorsal length of apical antennal segment about twice its width (cc), but 2.2–2.7 times in *P. mongolicus* from Rhodes and Corfu; frons flat medially (dd), but sometimes with a shallow longitudinal depression (ddd); sternites III-VII black basally (ee) and last sternite entirely black or nearly so (ff); apical half of antenna evenly orange or yellow dorsally (gg), but darkened in *P .albellus* (ggg); clypeus usually more or less curved medio-ventrally (hh) **29**



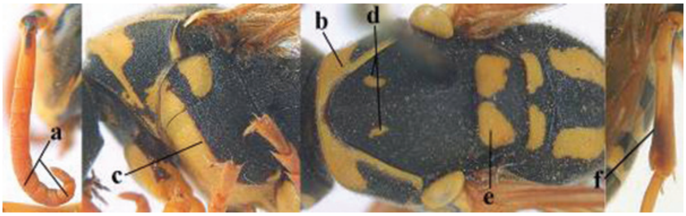
29 Malar space long, 0.8–1.0 times as long as width of third antennal segment measured basally (a, b); malar space often entirely yellow (c) or narrowly black posteriorly; [basal half of second sternite with yellow pattern; mesopleuron obliquely rugulose (d)] **30**



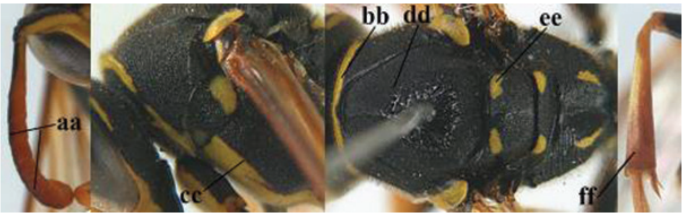
– Malar space short, 0.4–0.6 times basal width of third antennal segment (aa, bb); malar space black posteriorly with black area often widened (cc) **31**



30 Antenna dorsally orange-yellow (a); pronotal transverse yellow band more or less widened (b); epicnemial ridge delicate but well-defined (c), sometimes reduced in Peloponnesian populations; mesoscutum almost always with pair of medium-sized to large yellow spots (d), sometimes minute or absent; scutellar spots large (e); inner side of hind tibia often partly darkened (f); medial area of face narrower; N Italy to SE Europe, Turkey and Central Asia ....***P. foederatus* Kohl, 1898**



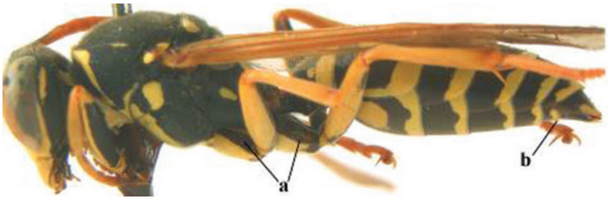
– Antenna dorsally dark brown (aa); pronotal transverse yellow band narrow (bb); epicnemial ridge indistinct (cc); mesoscutum with yellow spots minute or absent (dd); scutellar spots small (ee); inner side of hind tibia rather pale (ff); medial area of face wider; C Europe, temperate Asia ....***P. albellus* Giordani Soika, 1976**



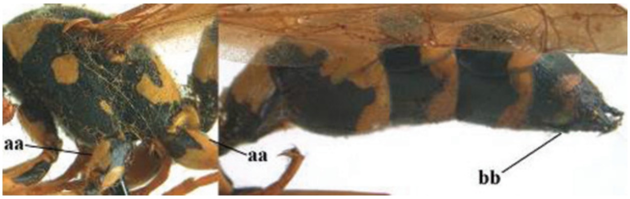
31 Specimens from W to C Asia, Cyprus, Egypt..**32**

– Specimens from Europe and NW Africa..**33**

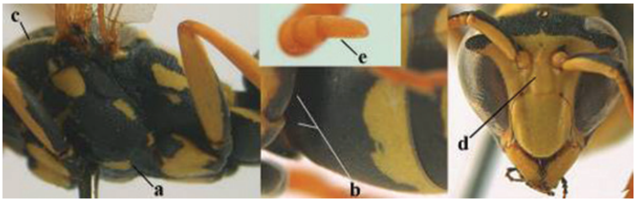
32 Middle and hind coxae largely black dorsally (a); apical yellow band of sternite VI medially interrupted (b); Turkey .... ***P. bischoffi* Weyrauch, 1937**



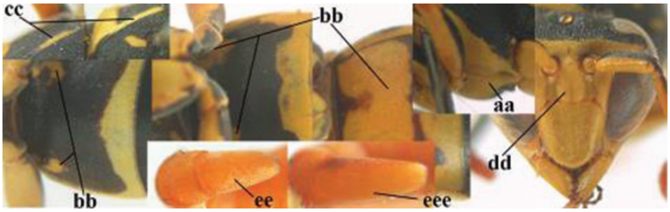
– Middle and hind coxae largely yellow dorsally (aa); apical yellow band of sternite VI medially continuous (bb); Cyprus, Turkey to Central Asia and Egypt... .... ***P. mongolicus* du Buysson, 1911**



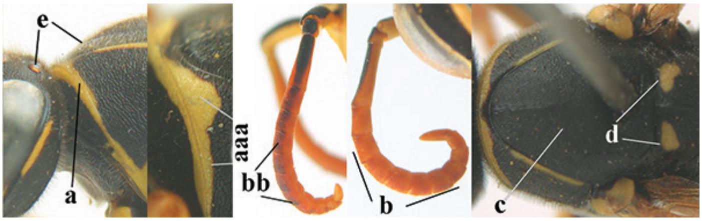
33 Mesosternum entirely black or with a pair of elongate yellow spots (a); basal half of second metasomal sternite entirely black (b); oblique yellow stripes of pronotum often long or medium-sized (c); frontal ridge narrower (d); apical antennal segment slightly slenderer and usually parallel-sided basally (e); SE Europe.............................***P. mongolicus* du Buysson, 1911**



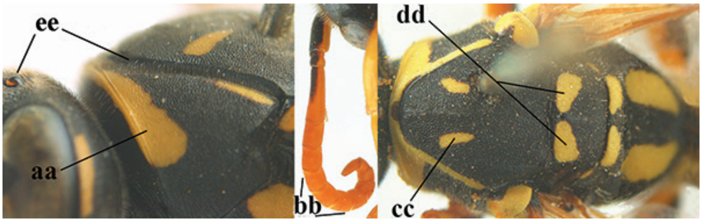
– Mesosternum predominantly or entirely yellow (aa); basal half of second sternite with yellow pattern, varying from a pair of very small sublateral yellow spots to mainly yellow (bb), **if** sometimes entirely black (*P. gallicus*) then pronotal transverse yellow band moderately widened; oblique yellow stripes of pronotum variable, sometimes absent (cc); frontal ridge wider (dd); apical antennal segment slightly less elongate and more or less widened basally (ee), but comparatively slender in *P. bischoffi* (eee) **34**



34 Yellow transverse pronotal band narrow laterally (a), **if** widened dorso-laterally then narrowed medio-laterally (aaa); apical half of antenna slightly infuscate (b), but if partly darkened dorsally (bb), cf. *P. albellus*; mesoscutum without or with minute paired yellow spots (c); scutellum usually with comparatively small paired yellow spots (d); setae of pronotum and mesoscutum 0.5–0.7 times diameter of posterior ocellus and curved (e); southern C and S Europe, Turkey .... ***P. bischoffi* Weyrauch, 1937**



– Yellow transverse pronotal band moderately to strongly widened laterally, of even width medio-laterally (aa); apical half of antenna uniformly orange to yellow dorsally and ventrally (bb), mesoscutum nearly always with minute to large paired yellow spots (cc); scutellum with large yellow spots (dd); setae of pronotum and mesoscutum usually shorter, about 0.5 times diameter of posterior ocellus and mainly straight (ee); NW Africa, SW Europe, N Italy, S Switzerland, Croatia, Corfu .... ***P. gallicus* (Linnaeus, 1767)**



Species treatments

Genus *Polistes* Latreille

Subgenus *Polistes* Latreille

Polistes Latreille, 1802, Hist. Nat. Crust. Insect. 3: 363. – Type species: *Vespa gallica* Linnaeus, 1767, designated by Latreille, 1810, Consid. Gén. Crust. Arachn. Insect.: 438.

Polystes [sic!]; Palisot de Beauvois, 1818, Insect. Recueill. Afrique Amérique: pl. 8; Buysson, 1892, Ann. Soc. Entomol. France 61: 59; H. von Ihering, 1896, Zool. Anz. 19: 452. Invalid emendation.

Eupolistes Dalla Torre, 1904, Genera Insect. 19: 68. – Name for "Premiere division" of *Polistes* Latreille in de Saussure, 1853, Et. Fam. Vesp. 2: 45 (61 species). Type species: *Vespa gallica* Linnaeus, 1767, designated by Richards, 1973, Rev. Bras. Entomol. 17 (13): 86.

Pseudopolistes Weyrauch, 1937, Zool. Jahrb. (Abt. Syst. Ökol. Geogr. Tiere) 70: 266, 274, genus (three species). – Unavailable; no type species designated.

Sulcopolistes Blüthgen, 1938 (1937), Konowia 16: 273. – Subgenus of *Polistes* Latreille. Type species: *Polistes semenowi* Morawitz, 1889, by original designation.

Polistula Weyrauch, 1938, Arbeit. Physiol. Angewand. Entomol. 5 (3): 273, genus (5 species). – Unavailable; no type species designated.

Polistula Weyrauch, 1939, Arch. Naturgesch. (N. F.) 8(2): 148. – Genus. Type species: *Polistes kohli* Dalla Torre, 1904 [= *Polistes biglumis* Linnaeus, 1758], by original designation.

Pseudopolistes Weyrauch, 1939, Arch. Naturgesch. (N. F) 8(2): 195. Validation by type selection of *Pseudopolistes* Weyrauch, 1937. Type species: *Polistes sulcifer* Zimmermann, 1930, by original designation.

Leptopolistes Blüthgen, 1943, Arch. Naturgesch. (N. F) 12(1): 99, 121. – Subgenus of *Polistes* Latreille. Type species: *Polistes associus* Kohl, 1898, by original designation.

Polistes albellus Giordani Soika

Fig. 1

Polistes bischoffi Weyrauch, 1937, Zoologische Jahrbücher (Jena), Abteilung für Systematik, Ökologie und Geographie der Tiere 70: 274, in part. – Mixed type series, see Neumeyer et al. (2014). Most citations of *P. bischoffi* from Central Europe refer to *P. albellus*.

Polistes foederatus albellus Giordani Soika, 1976, Acta zoologica Academiae Scientiarum Hungaricae 22(3–4): 272 – Holotype female (HNHM, currently on loan, not examined), type locality: Bulgan aimag: Namnan ul mountains, 23 km NW of Somon Chutag, Mongolia (1 paratype female in MSNV, examined by RN).

Polistes helveticus Neumeyer, 2014, ZooKeys, 400: 101-108. – Holotype female (NMBE, examined by RN), type locality: Schwerzenbach (Switzerland).

Polistes albellus – Neumeyer et al. 2015, Boletín de la Sociedad Entomológica Aragonesa (S.E.A.) 57: 206–211. – Species status.

Remarks. *Polistes albellus* was confused with *P. bischoffi* before Neumeyer et al. (2014) clarified the status of the latter by designating a neotype. He re-described the former under the new name *P. helveticus*. Later, Neumeyer et al. (2015) synonymised *P. helveticus* with *P. albellus*, a species described from Mongolia. Genetic results confirmed the conspecificity of the European populations with the Central Asian specimens (for detailed descriptions and discussion see Neumeyer et al. 2014, 2015).

The species typically occurs on humid meadows or along lake shores or in fens with a large reed zone, but it also colonizes dry habitats. In contrast to *P. biglumis*, *P. albellus* does not occur at higher altitudes of the Alps. Both species may sometimes occur sympatrically in lowland habitats.

Diagnosis. The female is characterized by reduced yellow markings and dorsally dark antennal segments. It can be confused mainly with *P. biglumis*. Distinction of

Figures 1–12. *Polistes* heads in frontal view. **1** *P. albellus* **2** *P. associus* **3** *P. atrimandibularis* **4** *P. austroccidentalis* sp. n. **5** *P. biglumis*, **6** *P. bischoffi* (Switzerland) **7** *P. bischoffi* (France) **8** *P. bucharensis* (Crete) **9** *P. bucharensis* (Turkey) **10** *P. dominula* (Germany) **11** *P. dominula* (Hungary) **12** *P. dominula* (Hungary).

the females of the two species is problematic and they are most easily separated by the lack of an epicnemial ridge in combination with an even transition in sculpture from the coarser sculptured mesopleuron to the finer sculptured epicnemium in *P. albellus*. *Polistes biglumis* is characterized by having an epicnemial ridge, with a sudden change from the rather coarse sculpture of mesopleuron to the finer sculpture of the epicnemium. In addition, the mesoscutal setae are shorter in *P. albellus* than in *P. biglumis*.

The male is unique within the *gallicus*-group by the combination of narrow temples (genae) in dorsal view and the antenna, with nearly black or dark brown dorsal surface. Females from Central Asia are darker than European individuals (clypeus may

Figures 13–24. *Polistes* heads in frontal view. **13** *P. foederatus* (Greece) **14** *P. gallicus* (Spain) **15** *P. gallicus* (Italy) **16** *P. maroccanus* sp. n. **17** *P. mongolicus* (Greece) **18** *P. mongolicus* (Croatia) **19** *P. mongolicus* (Croatia) **20** *P. nimpha* (Germany), **21** *P. nimpha* (Turkey), **22** *P. nimpha* (Turkey) **23** *P. nimpha* (Turkey), **24** *P. semenowi*.

be all black with small basal pale spot), and yellow markings are largely replaced by white or ivory.

Distribution. *Polistes albellus* has a wide distribution, ranging from eastern France to the Pacific coast of the Russian Far East, although latitudinally remaining roughly between the 44th (France, Lardiers: 44°03'N) and the 53rd (Russia, Donskoye: 52°03'N) northern latitude (Neumeyer et al. 2015). In Germany, the northernmost records are from central Hessen (Tischendorf et al. 2015) and Ebergötzen (Niedersachsen, 51°34'N 10°06'E, Neumeyer et al. 2015). The species usually occurs at elevations below 1000 m a.s.l.

Specimens examined. Europe: France (eastern part), Belgium, Switzerland, Germany, Austria, Czech Republic, Russia (Orenburg Oblast). Asia: Kazakhstan, Mongolia, Russia (Primorsky Krai), China.

Genetic results. Specimens from Switzerland, Germany, and regions as far apart as Kazakhstan exhibited little intraspecific variation (0.16%, Table 1).

Polistes associus Kohl

Fig. 2

Polistes associa Kohl, 1898, Ann. Naturh. Hofmus., Wien 13: 89 + Taf. III. – Syntypes males (NHMW, male from Poros examined by RN & CvA), type localities Poros (Greece) and "Helenendorf" [Göygöl], Azerbaijan. Male from Poros designated as lectotype by Blüthgen on label, but not in Blüthgen (1943: 121). The male is herewith designated, **new designation**.

Diagnosis. The recognition of *P. associus* females may be problematic because of their similarity to *P. nimpha*, in particular specimens from SW Asia. Females can be separated by colour differences only (see key to species), although in western Asia *P. nimpha* often exhibits high levels of colour variation.

The male is unique by the combination of narrow temples (genae) in dorsal view and a markedly depressed clypeus with distinct lateral ridges. The dorsal length of the apical antennal segment is about 3.0 times its maximum width, and longer than in similar species.

Distribution. Southern Europe and Turkey, northwards to Switzerland, southwards to Israel, eastwards to Azerbaijan. Guiglia (1972) also mentions India (Jammu and Kashmir) and China, but these records may refer to the similar species *P. chinensis* (Fabricius, 1793).

Specimens examined. Europe: Spain, France, Italy, Switzerland, Croatia, Bulgaria, Macedonia, Montenegro, Greece. Asia: Israel.

Genetic results. We regard *P. associus* as a member of the *P. dominula* group instead of the *P. gallicus* group due to the results of genetic data (see discussion below for details). Specimens from Croatia and northern Italy exhibited no intraspecific variation (Table 1).

Polistes atrimandibularis Zimmermann

Fig. 3

Polistes atrimandibularis Zimmermann, 1930, Mitt. Zool. Mus. Berlin 15: 611. – Holotype male (MFNB, examined by CSE), type locality: Toblach, "[Süd]Tirol 19.8.1908" (Italy).

Polistes atrimandibularis albidus Blüthgen, 1957, Revue de la Faculté des Sciences de l'Université d'Istanbul. Série B 22 (3): 164. Holotype male (MFNB, not examined), type locality: Ulu Dagh [Uludağ], Turkey. Probably a synonym of *P. atrimandibularis*.

Sulcopolistes atrimandibularis – Guiglia (1972), new combination.

Diagnosis. The social parasitic species can be recognized by the shape of the mandibular impression and by the colour pattern of the clypeus. Females of the species group show differences in the depth of the medial impression of the mandible and the size and shape of the upper ridge. The weakest medial impression occurs in *P. maroccanus*, whose upper ridge is only weakly developed or even lacking in the paratype. It is followed by *P. atrimandibularis* with a shallow impression, and flat, but visible upper ridges. The medial impression is deep in *P. austroccidentalis*, with large but not modified upper ridges, whereas in *P. semenowi* the impression is very deep with large and narrow upper ridges. Additionally, the lower ridge is modified with a triangular margin in dorsal view. The size of the black clypeal spot is variable but as a general rule it is largest in *P. austroccidentalis* (only upper third of clypeus yellow), medium-sized in *P. semenowi* (lower third black only), small and isolated in *P. atrimandibularis*, and even smaller (isolated) or completely lacking in *P. maroccanus*.

The shape of the mandibular impression in males generally follows that of females, but is in general less developed. In addition, the male of *P. atrimandibularis* has the mandible and parts of clypeus black (almost entirely so in some specimens, except lateral margins), whereas mandible and clypeus are yellow in the remaining species. The male of *P. maroccanus* is unknown.

Distribution. Southern C and S Europe, northwards to S Germany, Turkey, Iran, Armenia (Guiglia, 1972). Records from NW Africa probably refer to *P. maroccanus* sp. n. A male from the MFNB from "Ägypten [Egypt], Ehrenberg [leg.]" is probably mislabelled because Egypt is far outside the known range of the species.

Specimens examined. Europe: Bulgaria (Rhodope Mts), France, Greece, Italy (Alps, Abruzzi), Spain, Switzerland.

Biology. *P. atrimandibularis* is a social parasite of *P. biglumis*. In Greece, it was collected together with *P. biglumis* (2 males 20.ix.1989, Mt. Olympos, eastern slope, 2200-2500 m a.s.l., T. Osten leg., in coll. CSE).

Genetic data. Not enough specimens were sequenced to detect any genetic variation.

Polistes austroccidentalis van Achterberg & Neumeyer, sp. n.

http://zoobank.org/25A2E89A-26D5-414A-A5EB-7701EB831BDA

Figs 4, 25–45

Polistes semenowi auctt., nec Morawitz, 1889.

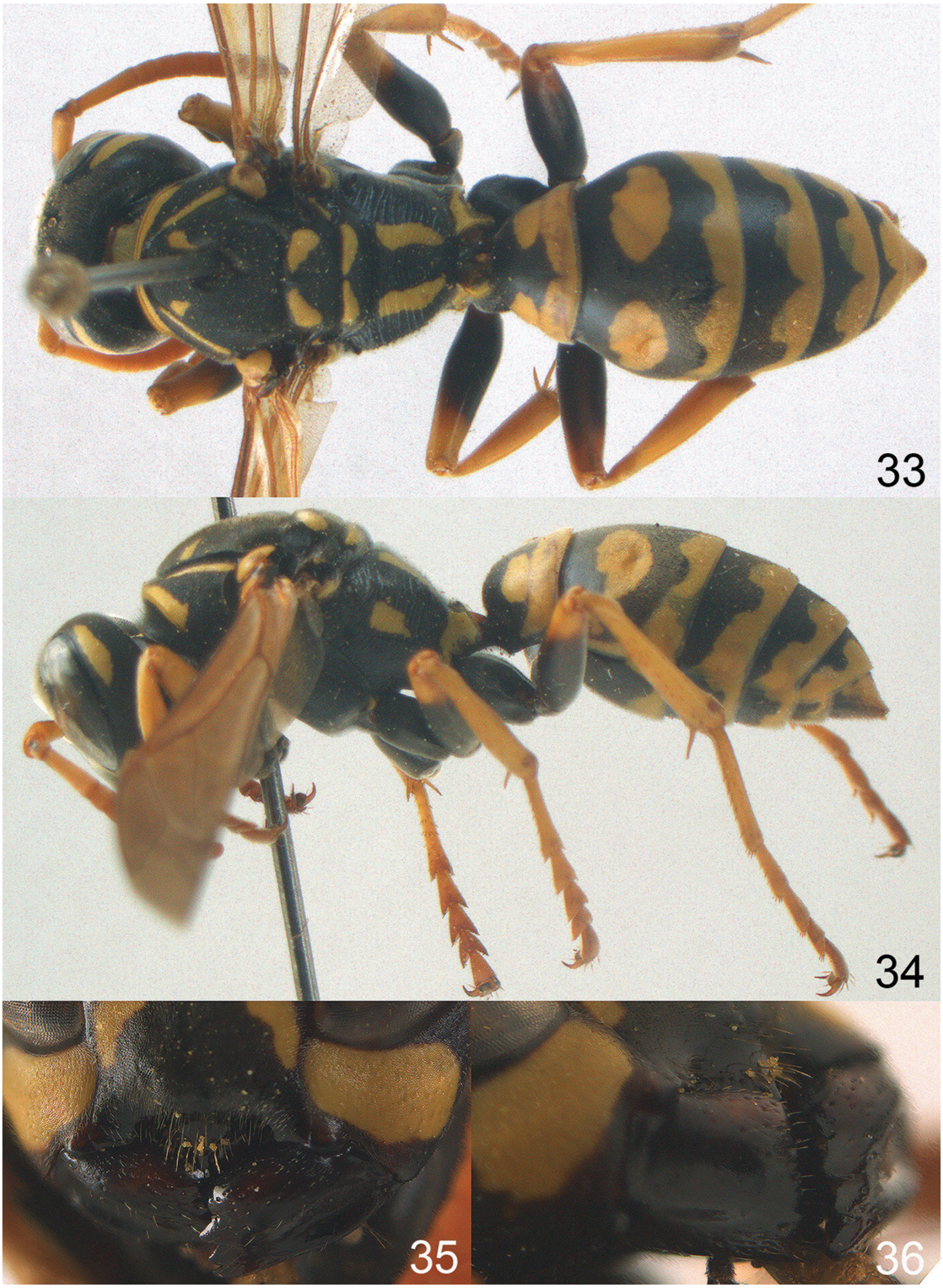
Type specimens. Holotype, ♀ (RMNH), "**España**, Burgos, Las Macharras, 23.iv.1984, R. Leys". Paratypes: 1♀ (RN0706), **Algeria**, Algiers, [unknown collector] (ETHZ); 1♂, Sid bel Abbes [unknown collector] (MFNB); 1♂, Blidah, Medeah, vii/viii.1884, Quedenfeld (MFNB); 2♀, **Andorra**, St. Julia, 21.vi.1981 & 1.v.1985, P.J.L. Roche (RMNH); 1♂ (GBIFCH00281850), **France**, Alpes-Maritimes, Lucéram, Peïra-Cava, 1400 m, viii.1950, Matthey (MZL); 1♀ (GBIFCH00281951), Bouches-du-Rhône, Eygalières, 13.viii.1964, D. Petitpierre (MZL); 1♂ (GBIFCH00281950), Saint-Rémy-de-Provence, 24.viii.1964, D. Petitpierre (MZL); 2♀, Camargue, Salin de Badon, 26.v.1952, H. Engel (RMNH); 1♀, id., but Astoin, 1.v.1981, R. Leys (RMNH); 1♀ (GBIFCH00281955), Haute-Savoie, Pied du Salève, 3. ix.1933, J. de Beaumont (MZL); 1♀, Hérault, Notre Dame de Londres, 8 km N of Les Matelles, 7.vii.1990, L. Blommers (RMNH); 1♀, Landes, Linxe, 21-30.vi.1968, R.T. Simon Thomas (RMNH); 1♀, Lot, Le Montat, 14-19.v.1986, A.D.J. Meeuse, on *Euphorbia* (RMNH); 1♀, Lozère, St. Enimie, Le Buisson, near Quézac, along Tarn, 21-28.vi.1986, P. Thomas (RMNH); 1♂, Vaucluse, Carpentras, 30-31.vii.1951, P.M.F. Verhoeff (RMNH); 1♀, Vaucluse, Bedoin, 1.vi.1993, H. & J.E. Wiering (RMNH); 1♀, id., but Rustrel, 300 m, 12.ix.1999 (RMNH); 1♀, Pyrénées-Orientales, Banyuls-sur-Mer, 5-200 m, 12.vii.1965, R.T. Simon Thomas; 1♀, Drôme, Espenel, 25.vii.1979, V. Lefeber (RMNH); 1♀, Montpellier/Lac du Salagou, 18.v.1986 & 1♀, 1♂, Narbonne plage, 11.ix.1987 & 1♂, Alpes Maritimes, Tende, 1000 m NN, 12.vii.2009 & 1♂, Pyrenees, Pic du Canigou, 1700 m, 13.ix.1987 & 1♂, Sisteron/Serres, 6.ix.1997, C. Schmid-Egger (CSE); 16♂ 25♀, Digne, 1957, Schewen, (ZSM), 1♂, 3♀, Champs de Bes, 1957, Schewen (ZSM) 1957; 1♀, Camargue, 13.vi.1852, Forster (ZSM); 1♂ (RN0690), **Italy**, Tuscany, Passo della Cisa ("Colle la Cisa"), 19.viii.1949, A. Nadig (ETHZ); 1♀, Aosta, 27.v.27, Bischoff (MFNB); 1♀ (RN0704), **Morocco**, Fès-Meknès, Ifrane, 22-24.vii.1932, A. Nadig (ETHZ); 1♂ (RN0722), Taza, 24.vii.1931, A. Nadig (ETHZ); 2♀ (RN0697, RN0699), 2♂ (RN0698, RN0723), Marrakesh-Safi, Asni, 10-14.vii.1932, A. Nadig (ETHZ); 1♂ (RN0705), Marrakesh, 6-18.vii.1932, A. Nadig (ETHZ); 2♀ (RN0700, RN0701), 2♂ (RN0702, RN0703), Tanger-Tétouan-Al Hoceïma, Tanger, 4.vii.1932, A. Nadig (ETHZ); 1♂, Atlas moyenne, Azrou, 2.vii.1926, Landshut (MFNB); 1♂, Aoulouz, 12.vi.2014 & 1♂, Haut Atlas, Aguelmouss, 13.vi.2014, 2070 m & 1♂, Haut Atlas, Tiz n'Tichka, 28.ix.2016, C. Schmid-Egger (CSE); 1♀, **Portugal**, C. Alentejo, Montfort, Vaiamonte, iii.2012, A. v. Harten (RMNH); 1♀, Porto, (MFNB); 1♀ (RN0721), **Spain**, Asturias, ≤ 1898, [unknown collector] (ETHZ); 1♀ (RN0695), Community of Madrid, El Escorial, R. García Mercet (ETHZ); 1♀ (RN0696), Rivas, J.M. Dusmet (ETHZ); 1♀, Alicante, Benidorm, 28.iv.1993, V. Lefeber (RMNH); 3♂, Granada, Sierra Nevada, near Albergue Universitario, 2500–2600 m, 16.vii.1953, C.A.W. Jeekel (RMNH); 1♂, id., but km 24 road Granada-Pic. de Veleta, 1700 m, 19.vii.1953, (RMNH); 1♂, Granada, Orgiva, 22.vii.1969, H. Overbeek (RMNH); 2♂, Santander, Enterrias, 30.viii.-5.ix.1969, M.C. & G. Kruseman (RMNH); 1♀, 1♂, Teruel, Albarracin, 27.ix.1963, (RMNH); 1♂, id., but 17.ix.1963 (RMNH); 1♂, Lerida, Artesa de Segre, 41°54'N, 1°3'E, 30.vii.1969, C. v. Heijningen (RMNH); 1♂, Málaga, Rincón de la Victoria, 6.vi.1967, M.J. & J.P. Duffels (RMNH); 1♀ Tiermas, viii.1926, Dusmet; 1♂,Villamartín, 30.vii.1950, Verhoeff; 1♂, Valle de Ordesa, vii 1923, Seitz; 2♀, Peña de Francia, Prov. Salamanca, Krichelsdorf; 1♀, Sta. Maria, Andalusia, vi.1993, Hering; 2♀, Aranjuez, 27.v.1920, Dusmet (MFNB); 1 ♂, San Fernando, 6.vi.1998, Kroupa (CSE); 1♀, Estepona [near Málaga], 1.-11.iv.1985, H. Wolf (C. Saure); 1 ♂ (RN0713), **Switzerland**, Canton Valais, Erschmatt, Bawald, 13.vii.2003, A. Breitenstein (ETHZ); 1♀ (GBIFCH00281987), Fully, Les Follatères, 11.vi.1932 & 1♀ (GBIFCH 00281986), 19.vii.1935, P. Bovey (MZL); 1♂ (RN0710), 12.viii.1941, A. Nadig (ETHZ); 2♂ (RN0711, RN0712), 23.vii.-2.viii.1942, A. Nadig (ETHZ); 1♀ (GBIFCH00281988), 13.v.1947, J. Aubert (MZL); 1♂ (RN0296), Gampel, Jeizibärg, 46°19’14.19"N, 07°43’53.53"E, 1090 m, rocky steppe, 10.viii.2013, R. Neumeyer (RN); 1♂ (GBIFCH00110807), Gampel, Jeizinen, 46°19’21.06"N, 07°43’50.81"E, 1200 m & 2♂ (GBIFCH00110810, GBIFCH00110811), 46°19’33.47"N, 07°44’02.57"E, 1330 m & 1♂ (GBIFCH00110809), 46°19’31.91"N, 07°43’36.85"E, 1430 m & 1♂ (GBIFCH00110808), 46°19’35.15"N, 07°43’36.86"E, 1480 m, 3.viii.2015, R. Wenger (RW); 1♀ (GBIFCH00281992), Martigny, viii.1932 & 1♀ (GBIFCH00281991), 29.viii.1933, R. Matthey (MZL); 2♀ (GBIFCH00281989, GBIFCH00281993), 29.iv.1934 & 1♀ (GBIFCH00281962), 28.iv.1935 & 1♀ (GBIFCH00281990), 14.vi.1936, J. de Beaumont (MZL); 1♂ (RN0707), Mörel, 19.viii.1916, [unknown collector] (ETHZ); 1♀ (GBIFCH00281985), Sierre, 26.v.1931, J. de Beaumont (MZL); 2♂ (RN0708, RN0709), 23.vii.-2.viii.1942, A. Nadig (ETHZ); 1♂ (RN0689), Stalden, ≤ 1893, [unknown collector] (ZMUZ); 1♂ (RN0714), ≤ 1893, [unknown collector] (ETHZ).

Remarks. Konstantin Samartsev (ZISP) kindly provided photos of the female lectotype of *P. semenowi* Morawitz, 1889, from Copet-dag. Their examination showed unambiguously that the specimen is conspecific with *P. sulcifer* (Zimmermann, 1930). This requires the species *P. semenowi* of authors to be described as a new species: *P. austroccidentalis* van Achterberg & Neumeyer, sp. n.

Diagnosis. Large and relatively bright species with robust mandible and wide, yellow malar space (Figs 29, 31, 35, 36), entirely yellow flagellum, black mesosternum and change in sculpture between mesepisternum and epicnemium rather abrupt (epicnemial ridge distinct) in both sexes. Outer face of mandible with distinct depression between a wide dorsal ridge and a much narrower ventral one; dorsal ridge of mandible convex and distinctly elevated above middle of mandible. Female clypeus mainly black, basally yellow (Fig. 29); mesoscutum with pair of yellow spots (Figs 26, 33); hind coxa black; yellow area along inner eye margin usually connected with yellow bar above antennal sockets (Fig. 29); hypopygium with yellow tip; basal half of mandible gradually curved in dorsal view and convex; clypeus abruptly depressed ventrally. Male with mandible mainly yellow, except for its more or less darkened margins (Figs 44, 45); mandibular depression rather short and occupying less than half of outer face of mandible, and dorsal ridge wide; clypeus medially entirely yellow, face and frons yellow (Fig. 42); temple (or gena) in dorsal view convex (Fig. 43). See also comments of *P. semenowi* for recognising the species.

Description. FEMALE. Holotype, body length 15.8 mm; fore wing length 11.6 mm. For colour pattern, see figures.

Figures 25–32. *Polistes austroccidentalis* sp. n. Holotype female. **25** Mesosoma in lateral view, **26** mesosoma in dorsal view **27** metasoma in lateral view **28** metasoma in dorsal view **29** head in frontal view **30** head in dorsal view **31** head in lateral view **32** fore wing.



Figures 33–36. *Polistes austroccidentalis* sp. n. Holotype female. **33** Habitus, dorsal view **34** habitus lateral view **35** lower part of head in frontal view **36** gena and mandibles.

Head. Mandible very stout and 1.5 times as long as wide (Figs 35, 36) and with a large depression on its outer face; basal half of mandible gradually curved in dorsal view and convex; dorsal ridge of mandible wide, smoothly convex without sharp edges and distinctly elevated above depression; ventral lobe of clypeus acute and step-like lowered; fine pubescence of clypeus conspicuous and comparatively long ventrally (Figs 29, 31); malar space 1.8 times POL; ocelli in equilateral triangle (Fig. 30).

Mesosoma. Posterior half of pronotum obliquely rugose and with short pubescence, only medio-anteriorly with longer setae; epicnemial ridge distinct and abruptly separating rugulose mesepisternum from smoothly sculptured epicnemium; propodeum coarsely transversely striate (Figs 25, 26). Fore wing distinctly infuscate anteriorly (Fig. 32), pterostigma and veins brown.

Variation. Body length 13.0–17.1 mm; fore wing length 10.1–12.7 mm. Mandible either black (Europe) or partially yellowish (NW Africa), if with a yellowish or brownish area then that area always smaller than yellow area on malar space. Vertex often with pair of tiny yellow spots behind lateral ocelli. Third antennal segment often with tiny basal dark brown spot, about 5% of specimens have the yellow posterior stripes of the pronotum connected to the transverse yellow band. Tergite II with paired antero-lateral yellow spots absent (NW Africa) or present (Europe). Hypopygium usually with yellow tip, but sometimes apical half or nearly entirely yellow, or entirely blackish and only dark brown apically.

MALE. Body length 11.6–17.1 mm; fore wing length 9.6–11.7 mm. For colour pattern, see figures. Similar to female, differs as follows:

Head. Mandible except for darkened margins yellow (Figs 44, 45). Clypeus yellow, and laterally distinctly convex, sub-antennal depressions continued onto clypeus (Fig. 44). Malar space yellow and 1.4 times as long as POL. Temples in dorsal view convex (Fig. 43). Face and anterior half of frons yellow, at most a tiny black spot on interantennal prominence and frequently also a narrow vertical black dash originating from upper margin of each torulus. Vertex often with pair of small yellow dots behind lateral ocelli, remainder of head black. Antenna brownish yellow, but scapus and pedicellus dorsally as black as a spot on third antennal segment (Figs 37, 42). Apical antennal segment 2.2 times as long as wide (Fig. 41).

Mesosoma. Mesoscutum with paired medium-sized yellow spots, sometimes reduced to tiny dots or absent (Figs 37, 39). Dorsal yellow spot of mesopleuron large but rarely minute, often only apex of femora yellowish.

Metasoma. Pair of spots of tergite I either connected to terminal band or well separated (Fig. 37). Sternites II-VI with continuous yellow terminal bands (Fig. 40), sometimes briefly interrupted on sternite VI. Hypopygium black with brown margin (Fig. 40).

Distribution. Specimens from Algeria, Andorra, France, Italy, Morocco, Portugal, Spain, and Switzerland have been examined, indicating that the species is confined to NW Africa and SW Europe with an extension to Central Europe, and is replaced by *Polistes semenowi* Morawitz further east. In Switzerland, *P. austroccidentalis* occurs only in

Figures 37–45. *Polistes austroccidentalis* sp. n. Paratype male. **37** habitus, dorsal view, **38** mesosoma in lateral view **39** mesosoma in dorsal view **40** metasoma in ventrolateral view **41** apex of antenna **42** head in frontal view **43** head in dorsal view **44** lower part of head in frontal view **45** gena and mandibles.

the SW part (Valais and one record in the Jura Mountains), whereas *P. semenowi* occupies mainly the SE part (Ticino and southern Grison valleys, except for two records from the canton of Valais).

Biology. According to Cervo (2006), *P. austroccidentalis* is an obligate social parasite, normally of *P. dominula*, but occasionally also of *P. nimpha*. Corresponding to its ubiquitous, euryoecious main host (*P. dominula*), *P. austroccidentalis* can be found in a wide variety of open and semi-open habitats, but up to now it apparently avoids the northern part of its host‘s range. The altitudinal records (n= 20) for *P. austroccidentalis* range from near sea level (Carpentras, France) to 2600 m in Spain (Sierra Nevada, Andalusia) and 2150 m in Morocco. The seasonal records (n = 67) range from March (Vaiamonte, Portugal) to 21 September in Switzerland (Ausserberg, VS) or 28. September in Morocco (males only), but most individuals were observed from May to August, at least in Switzerland (CSCF in litt.). There, the earliest record for males is 12 July (Erschmatt, VS), the latest for females 29 August (Martigny, VS).

Genetic data. Specimens from south-central Europe and Morocco only showed a small genetic distance.

Etymology. The name is a combination of the Latin adjectives “australis” (southern) and “occidentalis” (western), because of its southwestern distribution in Europe.

Polistes biglumis **(Linnaeus)**

Fig. 5

Vespa biglumis Linnaeus, 1758, Systema naturae 1 (Editio decima): 573. – Holotype female (LSL, examined by RN), designated by Day (1979), type locality: Europe.

Vespa rupestris Linnaeus, 1758, Systema naturae 1 (Editio decima): 573. – Holotype male (LSL, examined by RN), designated by Day (1979), type locality: Sweden.

Vespa bimaculata Geoffroy in Fourcroy, 1785, Entomologia parisiensis, sive catalogus insectorum quae in agro parisiensi reperiuntur, vol. 2: 433. – Holotype female (type lost; see Blüthgen 1961: 54), type locality: near Paris, France.

Polistes geoffroyi Lepeletier & Serville, 1825, In: Latreille M (Ed) Encyclopédie Méthodique, Histoire Naturelle. Insectes. Vol. 10: 173. – Syntypes males, females (MNHN, 1 female and 1 male examined by RN), type locality: France.

Polistes dubia Kohl, 1898, Annalen des kaiserlich-königlichen Naturhistorischen Hofmuseums, Wien 13: 90 + Taf. III. – Lectotype male (NHMW, examined by RN & CvA), designated by Blüthgen (1943: 128), type locality: Brühl, Austria.

Polistes kohli Dalla Torre, 1904, Vespidae. Genera Insectorum 19: 70. – Replacement name for *Polistes dubia* Kohl, 1898, nec de Saussure, 1867.

Polistes bimaculatus var. *arduinoi* Guiglia, 1948, Mem. Soc. Entomol. Ital. 27, Fasc. Suppl.: 14 (key), 22. – 2 syntype females (MSNG, not examined), type locality: Ponte di Legno, Lombardia (Italy).

Polistes pamirensis Zirngiebl, 1955: Mitt. Münchner Entomol. Ges. 44/45: 381–383. – Syntypes 4 females (ZSM, examined by RN), type locality: "Umss-Tugai", probably in the area of eastern Uzbekistan to southwestern Tadjikistan.

Polistes pamirensis var. *soikai* Zirngiebl, 1955, Mitt. Münchner Entomol. Ges. 44/45: 383. –Holotype female (ZSM, examined by RN), type locality: "Umss-Tugai", probably in the area of eastern Uzbekistan to southwestern Tadjikistan.

Polistes pamirensis var. *interruptus* Zirngiebl, 1955, Mitt. Münchner Entomol. Ges. 44/45: 383. – Holotype female (ZSM, examined by RN), type locality: "Umss-Tugai", probably in the area of eastern Uzbekistan to southwestern Tadjikistan.

Polistes bimaculatus var. *pamirensis* Zirngiebl, 1955: 385, var. status.

Polistes bimaculatus var. *nigrinotum* Zirngiebl, 1955, Mitt. Münchner Entomol. Ges. 44/45: 385. – Holotype female (ZSM, examined by RN), type locality: Althegnenberg, Germany.

Polistes biglumis alpium Blüthgen, 1957, Rev. Fac. Sci. Univ. Istanbul, Ser. B, 22 (3): 163. Holotype female (MFNB, examined by CSE). Type locality: Ulu Dagh [Uludağ], Turkey.

Remarks. See Neumeyer et al. (2014) for detailed comments about taxonomy.

Diagnosis. The female shares a dark brown to black upper side of antennal segments with *P. albellus* (see under *P. albellus* for recognition). The other species of the *P. gallicus* group have lighter antennal segments (except northern *P. foederatus*). The male has broad, convex temples in dorsal view and the clypeal disk without impressions or lateral ridges, similar to that of *P. dominula* and *P. bucharensis*.

Distribution. Europe including Norway and Sweden south of 65° N to Turkey, Central Asia. Guiglia (1972) also mentioned N Africa, Iran and Mongolia, but these records require confirmation. *Polistes biglumis* occurs up to 2400 m in the European Alps. The presence in Greece is confirmed by a male from Mt. Olympus, eastern slope, 2200-2500 m a.s.l., 20.ix.1989, leg. T. Osten, coll. CSE), removing doubts expressed by Arens (2011).

Specimens examined. Europe: Austria, Belgium, France, Germany, Greece, Italy, Netherlands, Sweden, Switzerland. Asia: Tajikistan, Turkey, Uzbekistan.

Genetic data. *Polistes biglumis* consists of two closely placed subclusters which share the same BIN (Suppl. material 2: NJ tree, and Fig. 58). Specimens from the Aosta valley in NW Italy form a geographic subcluster that is separated from a second subcluster consisting of specimens from NW Italy and SE Germany.

Polistes bischoffi Weyrauch

Figs 6, 7

Polistes bischoffi Weyrauch, 1937, Zoologische Jahrbücher (Jena), Abteilung für Systematik, Ökologie und Geographie der Tiere 70: 274. – Neotype female (NMBE, examined by RN, designated by Neumeyer et al. 2014), type locality: Galeria, Corsica (France).

Remarks. For a detailed discussion about the mixed type series of the species see Neumeyer et al. (2014, and references therein). Weyrauch (1937) described *P. bischoffi* from Sardinia and later (Weyrauch 1939) he included a dark form of *P. bischoffi* (actually *P. albellus*) that he interpreted as geographic variations (followed by Schmid-Egger and Treiber 1989, and others). The true *P. bischoffi* has a southern European distribution, whereas *P. albellus* ranges from Central Europe to the eastern Palaearctic region.

Diagnosis. This species belongs to the group of species with a short female malar space within the *P. gallicus* species group. The female can further be recognized by a medially interrupted yellow band on sternite IV, a large black spot or band on the clypeus, and by the dorsally black hind coxa. The sternal band IV is always continuous in *P. gallicus* and *P. mongolicus*, and the clypeus is entirely yellow in most *P. mongolicus* specimens or has a smaller, more excentric spot in most *P. gallicus* specimens. The epicnemial ridge is reduced or absent in *P. bischoffi* and *P. albellus* versus distinct or reduced in *P. gallicus* and *P. mongolicus*. The character is therefore of limited diagnostic value. The flagellum is in both sexes dorsally light orange to somewhat dark orange, whereas it is always light orange in related species, except northern *P. foederatus*. The male can be confused with *P. gallicus* (see the key to species for differences).

Distribution. S Europe and Turkey, northwards to Austria (Neusiedl am See) and Switzerland (northwards to Zürich). See Neumeyer et al. (2015) for the detailed distribution.

Specimens examined. Europe: Spain, Gibraltar, Switzerland, southern France and Corsica, Austria, Greece, Italy, Croatia. Asia: Eastern Turkey (Hakkari region).

Genetic results. Specimens from Spain, S France and Corsica, Switzerland, and Croatia were barcoded. The species forms a separate cluster, with a small gap between SW (France, Spain) and southern central European populations.

Polistes bucharensis Erichson, stat. rev.

Figs 8, 9

Polistes bucharensis Erichson, 1849, Mem. Acad. Sci. St. Petersburg (6)6: 307. – Holotype female (depository unknown), type locality: Uzbekistan "Bokhara" (= Bukhara). **Sp. restit.**

Polistes gallica var. *ornata* Weyrauch, 1938, Arbeit. Physiol. Angewand. Entomol. Berlin-Dahlem 5: 278, nec Lepeletier, 1836. – Female lectotype (lost), designated by Weyrauch (1939: 154), type locality: Astrabad [Gorgan], Iran. **Syn. n.** (previously considered a synonym of *P. dominula*)

Polistes gallica var. *pacifica* Weyrauch, 1939, nec Fabricius, 1804, Arch. Naturgesch. (N. F.) 8: 155–156. – Holotype female (depository unknown), type locality: China. Synonymy likely but requiring confirmation through examination of types.

Polistes gallicus pseudopacificus Giordani Soika, 1970, Ann. Hist.-Nat. Mus. Natl. Hung., Zool. 62: 326. Replacement name for *pacificus* Weyrauch, 1939, nec Fabricius, 1804.

Polistes iranus Guiglia, 1976, Boll. Mus. Civ. Stor. Nat. Venezia 28 (1976): 99; description of male and female. – Holotype female (MSNV, not examined), type locality „Daria Namak“ [salt steppe near Dariun], Fars (Iran). **Syn. n.**

Polistes gallicus muchei Gusenleitner, 1976, Nachrichtenbl. Bayer. Entomol. 25(6): 118. – Holotype male (OLL, not examined), type locality: “Kislovods” [Kislovodsk], northern Caucasus (Russia). Paratypes from Kislovodsk and from Turkey/Artvin. Six male paratypes (MFNB, examined by CSE). **Syn. n.** (previously considered a synonym of *P. dominula*)

Remarks and genetic data. *Polistes bucharensis* is recognized as a valid species distinct from *P. dominula* here. Its taxonomic status has been controversial. It was formerly treated as valid species (*P. iranus*) by Guigla (1976), as subspecies of *P. dominula* (e.g. Gusenleitner 1976), or as a synonym of *P. dominula* (Carpenter 1996). In our opinion *P. bucharensis* is clearly distinguishable from *P. dominula* by colour pattern, by shape of the male clypeus and by the genetic data.

Specimens from Mongolia and China (= *Polistes gallicus pseudopacificus*) probably belong to *P. bucharensis* and not to *P. dominula*, as indicated by Giordani Soika (1970).

The species was first described from Uzbekistan and later as *Polistes gallica* var. *ornata* and as *Polistes iranus* from Iran. It was not possible to examine types of these taxa, but their descriptions agree well with examined specimens. Also, we could examine a large series of specimens from the type locality of *P. bucharensis* from “Bukhara” in MFNB, which also agree with description of *P. bucharensis*. Therefore, the valid name for this taxon is *Polistes bucharensis* Erichson, 1849 sp. restit.; and *Polistes iranus* syn. n. is a new synonym of *P. bucharensis*.

Another problematic taxon in this group is *P. gallicus muchei*. It was described by Gusenleitner (1976) from northern Caucasus and eastern Turkey as a subspecies of *P. gallicus* (now *P. dominula*) based on reduced pale marks in the male and whitish yellow or ivory instead of yellow ground colour. Six male paratypes and a non-type male from eastern Turkey (Kars, identified by J. Gusenleitner as *P. gallicus muchei*, in coll. CSE) were examined by CSE. They agree with typical *P. bucharensis* by having the mesosternum black and the clypeal ridges present. The male from Kars differs by an all-black mesonotum and by a black medial spot on clypeus. Consequently, we treat “*muchei*” (based on males) as a dark and whitish colour form of *P. bucharensis* and not as a form of *P. dominula* (= former *P. gallicus*). It is probably restricted to mountainous regions of NE Turkey and the Caucasus. This assignment is based on colour and morphology alone and requires verification through sequence data.

According to the description by Gusenleitner (1976), the female paratypes of *P. muchei* differ markedly from typical *P. bucharensis* by a reduction of the pale body colour. The mesoscutum is black and the clypeus has a transverse band. We cannot rule out that the type series of *P. muchei* includes *P. nimpha* specimens. Two non-type females from Kagisman (eastern Turkey, collected by CSE together with the above-mentioned male) belong to two species: one to *P. bucharensis* (typical form) and other to *P. nimpha* (with extreme extended pale colour pattern: clypeus and genae all yellow, however, with the mesoscutum and the hypopygium (sternite VI) all black.

Based on the material that was available for us it appears that two taxa of this lineage occur in eastern Turkey and the Caucasus: *P. bucharensis* and *P. nimpha*. Males can be recognized easily by morphological characters (see key to species), whereas the identification of females is hampered by an extraordinary colour variation (extreme pale forms occur together with extreme dark forms). They can be distinguished by characters given in the key (mainly by colour of the hypopygium (sternite VI): yellow in *P. bucharensis*, mainly black or reddish in *P. nimpha*). In addition, the sculpture of the lower half of the mesopleuron is coarser in *P. bucharensis* than in *P. nimpha* (where it is finer, with overlap in a few specimens). Results of DNA barcoding of females is needed to confirm this hypothesis. Another problem is a white coloured form of *P. nimpha* in Iraq ("*P. nimpha irakensis*", see discussion under *P. nimpha*).

The MFNB houses a large series of females from West Pamir, collected in 1928 by Reinig. This taxon is darker than typical *P. bucharensis* from Bukhara or Turkey (yellow band on gena of female medially largely interrupted, mesoscutum black, tergites with narrow pale bands, and pale colour whitish instead of yellow). The specimens have the clypeus all whitish yellow, the clypeal disc is punctate with large punctures and has some bristles. They probably also represent a dark high-elevation form of *P. bucharensis*. The colour variation of Central Asian specimens is not understood well and requires examination of more material.

Three barcoded specimens from Crete were assigned a separate BIN (Tab. 1). Their colour pattern is intermediate between *P. bucharensis* and *P. dominula* (see description below) but genetically they are most similar to *P. bucharensis* from Cyprus. Therefore, we treat them as an island form of *P. bucharensis*. It is possible that the population from Crete represents a distinct species but further research is required to clarify the taxonomic status of the involved species.

The specimens barcoded fall into four clusters that were assigned three different BINs (Suppl. material 2: NJ tree). The species shows distinct geographic subclustering with specimens originating from Crete, Cyprus, and Azerbaijan. Specimens from Crete differ morphologically distinctly from those of Cyprus (see discussion above), whereas two of the examined specimens from Azerbaijan are similar to the specimens from Cyprus.

A single specimen from Azerbaijan has been assigned a different BIN, whereas another specimen from Azerbaijan that is morphologically similar to the remaining females of *P. bucharensis* agrees genetically with *P. dominula* from Central Europe (Suppl. material 2: NJ tree). More specimens from this region need to be examined to be able to assess the morphological variation of each potential species in this group and its status in relation to *P. dominula*. It is probable that several other genetically distinct taxonomic units of this *P. dominula*/*P. bucharensis* species complex occur in this region.

Diagnosis. *Polistes bucharensis* is similar to *P. dominula*, and both sexes can be distinguished by the continuous wide yellow band on the temple (gena); seen in lateral view it is more than half as wide as the temple and extends along the entire posterior margin of the eye (specimens from Crete are different, see below). In *P. dominula*, this band is medially interrupted and less than half as wide as the temple, rarely continuous but then it is constricted medially. In females, the yellow band above the antennae is always connected with the band along the inner eye margin. This band is isolated from the lateral bands in *P. dominula* and it does not reach the inner eye margin.

Females of *P. bucharensis* have an entirely yellow clypeus and a somewhat denser pilosity on the clypeus (the pilosity concerns the dark bristles on the clypeal surface). In females of *P. dominula* the colour of the clypeus is variable: entirely yellow (mainly in specimens from Central Europe) or with a black medial spot in 50-70% of specimens from southern Europe and western Turkey (fig. 38/39).

Sternite II is predominantly black with narrow apical yellow band in *P. bucharensis*, the visible part of the remaining sternites is entirely yellow (except in specimens from Cyprus, which have a larger basal part of sternite III black). In *P. dominula*, the visible base of the sternites III-V is always black and the apical yellow band is 0.5-0.7x as wide as the total visible part of the sternite. Additionally, the species can be recognised by the sculpture of the mesopleuron and the lateral face of the propodeum that is markedly coarser in females of *P. bucharensis* compared to *P. dominula*.

Males of *P. bucharensis* have the mesosternum always all black, whereas the mesosternum of *P. dominula* males is partly or entirely yellow. The mesosternum has at least two triangular yellow spots subapically (except in specimens from southern Greece, see below). The colour pattern of the sternites is more variable than in females. For distinction from *P. nimpha* and from species of higher mountains in Central Asia see the key to species and the discussion above.

Variations. Females from Crete (n = 6) differ from typical *P. bucharensis* by a reduction of the yellow body colour. The yellow band of the temple (gena) in lateral view is medially widely interrupted and the clypeus has nearly always a transverse band or medial spot (Fig. 35), except one female with entirely yellow clypeus. The yellow band above the antennal sockets is isolated from both lateral bands. Sternites III-VI are all yellow and sternite II has only a narrow yellow apical band.

The single male that was examined genetically has the mesosternum all black and the yellow band of the temple is medially interrupted. In specimens from Iran the yellow body colour of the only examined male from Arak is replaced by an extreme whitish yellow. For recognition of specimens from Caucasus and E Turkey see discussion on *P. dominula muchei*.

Distribution. From Central Turkey to Central Asia, Israel, Iran and Egypt. In Europe only known from Crete and Cyprus. Specimens described from China and Mongolia (not examined) may also belong to *P. bucharensis* (see Giordani Soika, 1970).

Specimens examined. Europe: Greece (Crete), Cyprus. Asia: Turkey (Diyarbakir, Hakkari, Van, Esendere, Mersin, Göreme, Kars/Kagisman), Iran (Arak/Besril), Azerbaijan, Uzbekistan (Bukhara), Israel (Arava Valley). Africa: Egypt (female, Oasis Dakhla, 2.ix.1992, CSE).

Polistes dominula (Christ)

Figs 10–12

Vespa dominula Christ, 1791, Naturgesch. Insect.: 229–232 + Taf. 21, fig. 1. – Types (♀,♂) lost, type locality: "Kronenberg an der Höh" [Kronberg im Taunus], Germany.

Polistes italica Herrich-Schäffer, 1840, Nomencl. Entomol. 2: 196. – Nomen nudum.

Polistes pectoralis Herrich-Schäffer, 1841, Fauna Insect. German. 179: 39 – Type (♂) lost, type locality: Italien [Italy].

Polistes gallica var. *Lefebvrei* Guérin, 1844, Iconographie du règne animal de G. Cuvier 3: 447 + Pl. 72, Fig. 6. – type repository unknown, type locality: Egypt.

Polistes maculatus Rudow, 1889, Societas Entomologica 3: 171. – Uncounted syntypes (type depository unknown), type locality Smyrna [Izmir], Turkey. The nest ("befestigt an einem Schilfrohrstengel" [attached on a reed stalk]) from where the syntypes were taken puts this synonymy in doubt.

Polistes Merceti Dusmet, 1903, Memorias de la Sociedad Española de Historia Natural 2 (3): 146 (key), 149. – Holotype male (not examined), type locality: Los Molinos, Madrid (Spain).

Polistes gallicus var. *rufescens* du Buysson, 1912, Annales d'Histoire Naturelle Délégation en Perse II. Entomol. 1: 79. – No type designated, neither type locality nor type depository mentioned. No specimens labelled as "*Polistes gallicus* var. *rufescens*" exist at the MNHN (Paris).

Remarks and genetic data. *Polistes dominula* and the reinstated closely related species *P. bucharensis* show high levels of variation in their colour patterns. Previously, both taxa were treated as a single species (Gusenleitner 1976, Carpenter 1996). Our study revealed the presence of six genetic clusters for the two species, all of which were assigned different BINs by the BOLD system, viz. 1) Morocco, 2) SW to Central Europe (subsequently referred to as western cluster), 3) SE to C Europe (subsequently referred to as eastern cluster), 4) Crete, 5) Cyprus to Azerbaijan, and 6) Azerbaijan (Table 1, Suppl. material 2: NJ tree with clusters 1–6 indicated by numbers next to each cluster). In both, the neighbour-joining and the phylogenetic analysis (Fig. 58, see below), *Polistes bucharensis* is nested within the *P. dominula* cluster.

Two of these clusters (2 and 3) occur in Europe. The current data indicate for cluster 2 a south-western European distribution although we could only examine one specimen from France and records from Spain still are missing. The cluster occurs over whole Germany and it is close to the cluster of Morocco (1). The other European cluster (3) includes specimens from Greece and Azerbaijan and seems to have a more south-eastern distribution. It covers whole Germany with the westernmost records from the Aosta valley in the Italian Alps. This cluster is genetically closer to *P. bucharensis* than to the *P. dominula* clusters (1) and (2) from the western area and consequently we treat specimens from Crete as *P. bucharensis* (see above).

The high intraspecific variation (Table 1) and presence of multiple BINs could be the result of several species being present. However, specimens from NW Africa and Europe are very similar and indistinguishable by morphology or colour pattern. Furthermore, Neumeyer at al. (2014) found no sufficient differences in the ITS1 gene between the European clusters 2 and 3. We therefore refrain from describing each cluster as a new species until further evidence is available.

Polistes bucharensis with its eastern clusters (3–6) is genetically closer to the eastern clusters of *P. dominula* (1, 2). However, specimens of *P. bucharensis* are clearly separated by colour pattern and male morphology from *P. dominula*, supporting the notion that they represent distinct species.

The population of Crete seems to be isolated from the remaining populations for a long period, and the common ancestor probably came from the *P. bucharensis* lineage.

Because of this result, we follow the concept of morphospecies here and treat *P. bucharensis* as a valid species, separated from *P. dominula* s. str. by genetics, morphology, and colour pattern.

Diagnosis. *Polistes dominula* is the most common *Polistes* species in Europe. The female is characterised by a mostly or entirely yellow sternite VI in combination with an orange apical half of the antenna. The yellow band on the temple behind the eye in lateral view is interrupted in nearly all examined specimens, except in some from southern Greece and from Tunisia. The clypeal pattern is variable. Populations from Central Europe usually have an all yellow clypeus, most specimens from southern Europe and some from southern Central Europe (e.g. southern Germany) have one or two black medial spots, or a band on the clypeus medially (Figs 38, 39).

The female of *P. dominula* can be confused with *P. associus* (see key to species) and with *P. bucharensis* in western Asia. *Polistes bucharensis* always has a completely yellow clypeus in combination with a continuous band on the temple behind the eyes. This band is interrupted in most specimens of *P. dominula*, and the clypeus has often (about two-thirds of examined specimens) black spots or a band in females from southern Europe. For specimens from Crete, see under *P. bucharensis*.

The male of *P. dominula* is characterised by the orange apical half of antenna in combination with the lack of any impressions or ridges on the clypeus. It can be distinguished from the similar *P. bucharensis* by a (partly or entire) yellow mesosternum; the latter is all black in *P. bucharensis*. Also, the clypeus is laterally somewhat bulging in *P. bucharensis*, and always without any elevations in *P. dominula*.

Some specimens of *P. dominula* (identity confirmed by barcoding) from the Peloponnese (Greece) have some colour similarities of typical *P. bucharensis* (females with yellow clypeus and with wide yellow band on temple, males with mesosternum entirely black) and resemble *P. bucharensis*. However, the yellow band on the temple is medially constricted, and the yellow band above the antennal sockets is isolated from both lateral bands. In addition, the mesopleural sculpture is finer than that of typical *P. bucharensis*. We therefore regard these specimens as pale form of *P. dominula* at the SE border of its distribution area. The specimens from Greece occur together with typically coloured *P. dominula* (females: clypeus with large black spot or band, band on temple interrupted; males: mesosternum partly or all yellow). A female from Tunisia

(Dougga) agrees in colour pattern with the above-described pale females from Greece and likely belongs to the same whitish form of *P. dominula*.

Distribution. NW Africa, C and S Europe as far north as Latvia, but missing in Great Britain, Scandinavia, Crete and Cyprus. Introduced to Australia, North America (including Canada, Buck et al. 2008) and South America. The species has also been recorded from central and eastern Palaearctic regions and from India (e.g. Guiglia 1972). These records need confirmation, because they may belong to *P. bucharensis*. The easternmost records that we could examine are from western Turkey and from Azerbaijan. However, it can be expected that the species occurs farther east in Russia or Central Asia. One examined female from Egypt is clearly *P. bucharensis* and *P. dominula* probably does not occur in NE Africa.

Specimens examined. Europe: Examined from most countries in Central and S Europe. Asia: Turkey (Termessos/Antalya), Azerbaijan. Africa: Morocco, Tunisia.

Polistes foederatus **Kohl, sp. restit.**

Fig. 13

Polistes foederata Kohl, 1898, Annalen des kaiserlich-königlichen Naturhistorischen Hofmuseums, Wien 13: 90 + Taf. III. – Lectotype male (NHMW, examined by RN & CvA), designated by Blüthgen (1943: 129), type locality "Transkauk., Helenendorf" [Göygöl], Azerbaijan. **Sp. restit.**

Polistes foederata var. *obscuricornis* Mader, 1936, Entomologische Zeitschrift (Frankfurt a.M.) 50 (23): 263. – 2 syntype females (NHMW, examined by RN & CvA), type locality: Insel Krk [island of Krk], Croatia, but the name is not available (A. Ćetković, in litt.).

Remarks. The species is widespread in N Italy, the Balkans, and western Asia (Turkey to Caucasus area). The identity of *P. foederatus* remained unclear for a long time, and in the past the species was usually treated as *P. gallicus*. Arens (2011) was the first to recognize two species of the *P. gallicus* group in Greece (*P. gallicus* and *P. hellenicus*), using the length of the malar space as a new diagnostic character. However, he interpreted specimens with long malar space as "*P. gallicus*" but ignored that true *P. gallicus* from the western Mediterranean usually have a short malar space (with some exceptions). Type examination and genetic analysis clearly show that *P. gallicus* sensu Arens (2011) from Greece belong to *P. foederatus*.

Diagnosis. *Polistes foederatus* is unique in the *P. gallicus* species group by possessing the longest malar space of all species combined with a large and mainly rectangular and central black spot on the clypeus in females. In addition, the dorsal side of the flagellum is often slightly darkened. However, especially females can be confused with *P. gallicus* in the transition zone of both species (N Italy to Balkans), because the latter rarely has an extreme long malar space (some genetically examined specimens from the Italian Alps). The flagellum is completely reddish in *P. gallicus*, but always darkened dorsally in alpine *P. foederatus*. The yellow spots on the mesoscutum are usually lacking in smaller specimens from Croatia and Italy. The male is variable in colour pattern; the mesoscutum is black or has a pair of large yellow spots and the base of tergite II is either black or largely yellow.

Distribution. From NE Italy to Greece and Azerbaijan. Widespread and common in mainland Greece (Arens 2011, as *P. gallicus*).

Specimens examined. Europe: Italy (Trentino/Rovereto, Lombardia/Valtellina/Grossio, Veneto/N of Verona), Croatia (Krk), Greece (Crete/Matala, Peloponnese), Cyprus (Akrotiri). Asia: Turkey (Antalya), Azerbaijan.

Genetic data. Specimens of *Polistes foederatus* from several countries, including Azerbaijan, where the type locality is situated, were analysed genetically. The species exhibits little genetic variation and all specimens share the same BIN. The specimens from Crete form a distinct subcluster, perhaps because of longer isolation. However, the specimens from Crete are closer to specimens from the European and Asian mainland than Cretan *P. bucharensis* are from their mainland populations.

***Polistes gallicus* (Linnaeus)**

Figs 14, 15

Vespa gallica Linnaeus, 1767, Systema Naturae Ed. 12, 1 (2): 949 – Holotype male (LSL, examined by RN), type locality "Europa australi" [S Europe].

Polistula omissa Weyrauch, 1938, Arbeiten über physiologische und angewandte Entomologie aus Berlin-Dahlem 5 (3): 277 – Lectotype male (lost; see Arens 2011: 462), designated by Weyrauch 1939, Archiv für Naturgeschichte, Neue Folge 8 (2): 161, type locality: Marseille, France, mentioned in Weyrauch (1939: 161).

Remarks. The name *P. gallicus* (sensu lato) was used in the past for three Mediterranean species: *P. foederatus*, *P. mongolicus,* and *P. gallicus*. A reassessment of morphological characters in combination with DNA barcoding shows that *P. gallicus* (sensu stricto) is a valid species with a mainly western Mediterranean distribution (eastwards to Corfu, but probably very rare on Balkans). *Polistula omissa* is regarded as a synonym of *P. gallicus* (sensu stricto).

Diagnosis. *Polistes gallicus* females are characterised by a short malar space (but in a few specimens from Italy as long as in *P. foederatus*) and by two yellow spots on the mesoscutum; these spots are absent in most females of *P. mongolicus*. If there is a dark patch on the clypeus, it is small (rounded or forming a transverse band) and situated on the apical half of the clypeus. The posterior pronotal band is variable, short (in most specimens from Portugal) or reaching the anterior pronotal transverse band (in most specimens from N Italy). In the transition zone to *P. mongolicus* (N Italy, Balkans), *P. gallicus* can be confused with *P. mongolicus* when the yellow mesonotal spots are absent (one barcoded female of *P. gallicus* from Italy, Lombardia, with reduced, minute yellow spots only). *Polistes gallicus* has the posterior stripes connected to the anterior transverse band of the pronotum, whereas it remains separated from the pronotal band in all examined *P. mongolicus* from Croatia. Males can be recognized by the combination of the short malar space and two yellow spots on the mesoscutum.

Colour variation. All examined females from NW Africa have the clypeus yellow (one female with minute black spot), the mesoscutum has a pair of large yellow spots, and the tergite VI is entirely black (apical half yellow in one specimen). Males from NW Africa were not examined.

Distribution. Western and central Mediterranean area, eastwards to the Greek island of Corfu. In NW Africa from Tunisia to Morocco. Northwards to Italian Alps and S Switzerland. Specimens from Egypt and Israel formerly assigned to *P. gallicus* belong to *P. mongolicus*.

Specimens examined. Europe: Croatia (Istria), Greece (Corfu), Italy (Lombardia/Brescia, Veneto/N. of Verona, Pavone, Dro, Sardinia), Spain (Mallorca/Alcúdia, Andalucía/various locations), France (Bouches du Rhône/Alpilles, Pont du Diable, La Rouquette), Portugal (Algarve/Carrapeteira), Malta (Ghajn Tuffieha, female, photo from Kristofer Mogyorossy), Switzerland. Africa: Algeria (Alger), Morocco (Sefrou, Ht Atlas), Tunisia (Le Kef).

Genetic results. Specimens from *Polistes gallicus* originating from several European countries between Croatia and Portugal and from Morocco were examined genetically. They exhibit some genetic variation but all specimens share the same BIN.

Polistes maroccanus Schmid-Egger, sp. n.

http://zoobank.org/BCA5FEA8-A64F-48AD-8203-7350DE1BC870
Figs 16, 46–56

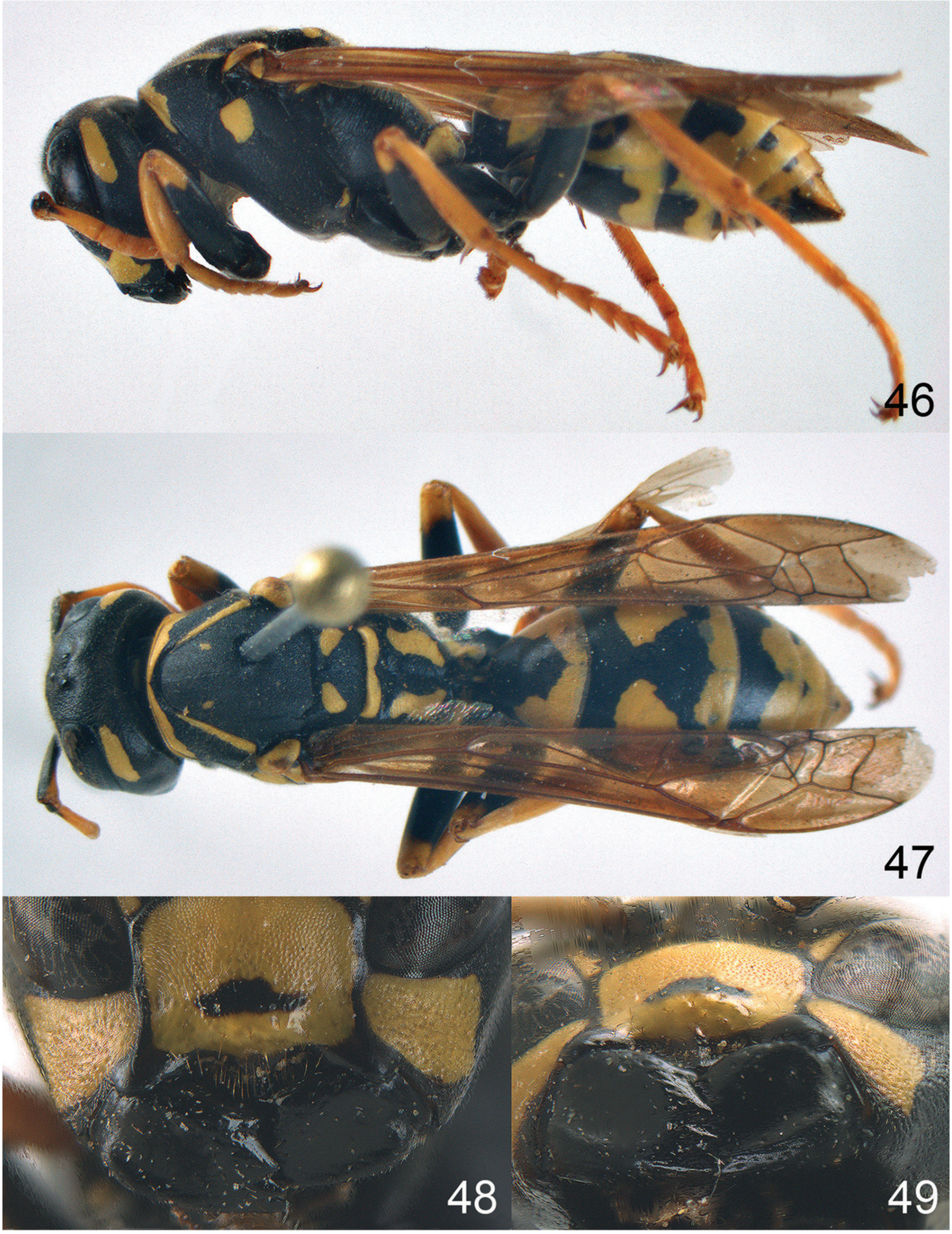
Type specimens. Holotype♀, Morocco, Haut Atlas, 2 km N Tizi n'Tichka, 31.289°N, 7.381°W, 2150 m 13.vi.2014, (leg. Schmid-Egger, voucher ID: BC ZSM HYM 22043, ZSM). Specimen with right antenna and right fore leg missing. Paratypes: 1♀, Ifrane env. 9.v.1997, (leg. Denes jun., coll. OLL). 1♀ (RN0664), Asni (1250 m), 3-11 vii 1934 (A. Ball leg., ETHZ).

Diagnosis. *Polistes maroccanus* sp. n. is close to *P. atrimandibularis* and can be distinguished by the characters given in Table 2.

Description. FEMALE. Holotype, body length 14 mm; fore wing length 11.5 mm. For colour pattern see figures.

Head. Mandible with a large depression on its outer face; both ridges of mandible narrow, medially 0.15 times as wide as mandibular diameter, remaining space shiny, with a few large punctures on upper third; malar space 1.5 times POL. Clypeus slightly wider than long (length/width ratio 0.92 in holotype, 0.86 in paratype).

Mesosoma. Posterior half of pronotum obliquely rugose and with short pubescence, only medio-anteriorly with longer setae; change in sculpture between mesepisternum and epicnemium abrupt (="epicnemial ridge distinct"), mesepisternum densely rugu-



Figures 46–49. *Polistes maroccanus* sp. n. Holotype female. **46** habitus, lateral view **47** habitus, dorsal view **48** lower part of head in frontal view **49** head in ventral view.

lose and epicnemium only superficially micro-sculptured; propodeum coarsely transversely striate. fore wing including pterostigma and veins reddish brown.

Variations. Body length of paratypes similar to holotype. Left mandible of one paratype with small yellow spot, and clypeus all yellow in one paratype.

Figures 50–56. *Polistes maroccanus* sp. n. Holotype female. **50** mesosoma in lateral view, **51** mesosoma in dorsal view **52** metasoma in dorsal view **53** metasoma in ventrolateral view **54** head in frontal view **55** head in dorsal view **56** head in lateral view.

Table 2. Characters for separating *P. maroccanus* from *P. atrimandibularis* (females only, HT = Holotype, PT = Paratype).

Lower ridge of mandible narrow, in HT= 0.22× (in PT= 0.24×) as large as mandible (measured medially)	Lower ridge of mandible wider, 0.37× as wide as mandible
Both ridges of clypeus smaller, upper ridge in PT nearly flat and barely expressed	Both ridges of clypeus wider
Medial impression of mandible shiny, with very fine microsculpture	Medial impression of mandible dull, with coarser microsculpture
Lower margin of clypeus (= near margin of yellow colour) ridged, shiny	Lower margin of clypeus straight, with microsculpture
Mesoscutum in HT medially with two minute yellow spots, black in PT	Mesoscutum all black
Black clypeal spot band-shaped, small in holotype, missing in paratypes	Black clypeal spot larger

Distribution. Only known from the High and Middle Atlas Mountains in Morocco. Previous to this study, CSE identified a female from Quirgane (High Atlas, 22.v.1995, leg. et coll. M. Hauser) as *P. atrimandibularis*. It is probably referable to *P. maroccanus* as well but the specimen was not available for re-examination.

Biology. The species is most probably a social parasite. At the type locality, it was collected together with *P. dominula* that is most probably the host.

Etymology. *Polistes maroccanus* is named after the country of origin, Morocco.

Remarks. DNA barcoding of a specimen from Morocco, formerly identified as *P. atrimandibularis,* indicated that it belongs to a different species that is close to the previously known social parasites. A detailed morphological examination resulted in some different character states and supports the notion that the Moroccan specimens belong to a new species. The species is morphologically close to *P. atrimandibularis* and probably replaces it in NW Africa.

Polistes mongolicus du Buysson, stat. rev.

Figs 17–19

Polistes gallicus var. *mongolicus* du Buysson, 1911, Bulletin du Muséum National d'Histoire Naturelle 76: 218 – Syntypes males, females (MNHN, ZISP, male from MNHN examined by RN & CvA, hereby designated as lectotype by CvA), type locality: road from Kuqa ["Koutchar"] to Karashahr ["Karachar"], China (Xinjiang autonomous region), ix.1909. **Stat. rev.**

Polistes omissus var. *ordubadensis* Zirngiebl, 1955, Mitt. Münchner Entomol. Ges. 44/45: 381. – Holotype female (ZSM, examined by RN & CvA), type locality: Ordubad, Azerbaijan. **Syn. n.**

Polistes omissus kaszabi Giordani Soika, 1970: 327–328 – Holotype female (HNHM, examined by RN), type locality "Duusch ul" near Züünkharaa ["Zuun-Chara"], Mongolia. Synonymy tentative.

Polistes hellenicus Arens, 2011: 464 – Holotype male (coll. Werner Arens, examined by RN), paratype (examined by CvA), type locality: Ano Kotili, Greece. **Syn. n.**

Remarks. The species is widespread in SE Europe to C Asia and China. Apart from the original description it was later described as *P. omissus* var. *ordubadensis* Zirngiebl from Caucasus and as *P. hellenicus* from Greece by Arens (2011). Arens (2011) was the first who recognized two different species of the *P. gallicus* species group in Greece and he described *P. hellenicus* as new species. He based his description mainly on the short malar space in contrast to *P. foederatus* with long malar space, and the black venter of the males (yellow in *P. foederatus*). Morphological comparison, genetic examination of specimens from a wide geografic range and type study confirms the conspecificity of *P. hellenicus* and *P. ordubadensis* with *P. mongolicus*. Our material increases the known range of the species from Croatia to Central Asia and China, and to NE Africa. The examined type specimen of *P. mongolicus* from China is somewhat darker than western specimens, but agrees in general aspects with our species definition. For taxonomic status of *Polistes omissus kaszabi*, see Neumeyer et al. (2014).

Diagnosis. Within the *P. gallicus* group the female of *P. mongolicus* is characterized by a short malar space, the lack of yellow spots on the mesoscutum (present in some females from Greece and western Asia), and usually by a yellow clypeus. Some females mainly from Greece have a very small to a medium-sized transverse spot on the clypeus. See Arens (2011, as *P. hellenicus*) for discussion of the colour variability. *Polistes foederatus* has longer malar space (see key to species).

The recognition of *P. mongolicus* is not problematic in Greece and farther east, but on the Balkans females may be confused with *P. gallicus* (see diagnosis of the latter). Males of *P. mongolicus* occur in two different colour forms. Specimens from Europe usually have the mesosternum entirely black or with a pair of yellowish spots, whereas the mesosternum of males from Asia and Egypt is largely yellow. Recognition of European males is therefore unambiguous.

In N Africa *P. mongolicus* is restricted to Egypt, whereas *P. gallicus* occurs in Tunisia, Algeria and Morocco. Specimens from Libya were not examined, but it cannot be ruled out that ranges of both species overlap in this region.

Colour variations. All examined females from Egypt have a yellow clypeus, with at most a minute black medial spot; the hypopygium (sternite VI) is partly yellow or reddish; one of the females has a pair of minute yellow spots on the mesoscutum.

Distribution. Balkans from Croatia to Greece, east to Central Asia, Mongolia, and China, south to Israel and Egypt.

Specimens examined. Europe: Croatia, Serbia, Macedonia, Greece, Cyprus. Asia: Turkey (Antalya, Hakkari), Israel (Jordan Valley), Azerbaijan, China. Africa: Egypt (Kairo; Al Fajum).

Genetic results. Specimens from Croatia, Greece, Turkey, Cyprus, and Azerbaijan were analysed. *Polistes mongolicus* shows some genetic divergence, mainly between specimens from Cyprus, from Asia and from Europe, with a mean intraspecific distance of 0.88% and a maximum intraspecific distance of 2.04% (Table 1). They all share the same BIN.

Polistes nimpha (Christ)

Figs 20–23

Vespa nimpha Christ, 1791, Naturgesch. Insekt.: 232. – Types (female, male) lost, type locality: Kronberg, Taunus (Germany).

Vespa diadema Latreille, 1802, Ann. Mus. Hist. Nat. 1: 292, nec Christ, 1791. – Type (female) lost, type locality: surroundings of Paris (France).

Polistes opinabilis Kohl, 1898, Ann. Naturh. Hofmus., Wien 13: 90 + Taf. III. – Lectotype male (NHMW, examined by RN & CvA) designated by Blüthgen (1943: 127), type locality: Frain [= Vranov], Moravia (Czech Republic).

Polistes nimpha var. *Moltonii* Guiglia, 1944, Atti d. Soc. Italiana di Sc. Nate del Museo Civico di Storia Naturale in Milano 83: 166. – Holotype female (MSNM, not examined), type locality: Spotorno, Liguria (Italy).

Polistes nimpha irakensis Gusenleitner, 1976: 119. – Holotype male (ZSM, examined by CSE), type locality “Hashimiya, Irak”. Female paratype from Abu Ghureib, Iraq, (ZSM, examined by CSE).

Remarks. *Polistes nimpha* is well defined by male morphology, in particular the long apical antennal segment and distinct lateral ridges of the clypeus, and in the female by the colour pattern (European specimens only). In western Asia, the recognition of females is not always easy since the species varies markedly in colour pattern. It can be confused with *P. associus* (lowlands of Turkey, Israel) and with *P. bucharensis* (eastern Turkey, Caucasus region, Iraq). In a small geographic area in western Asia, the dark and the pale coloured form occur in close vicinity, but probably not sympatric. Especially specimens from Iraq have an extended yellow colour pattern and can be confused with *P. bucharensis*. They can be recognised by the colour of the hypopygium (=sternite VI), but identification of some females remains difficult.

Differences in the ocellar angle (more obtuse in *P. nimpha/dominula* than in *P. associus*), as stated by Arens (2011), cannot be confirmed here. The sculpture of the lower half of the mesopleuron is somewhat coarser in *P. nimpha* than in *P. associus*, although both species overlap in this character.

Diagnosis. The most important diagnostic character of *P. nimpha* females is the shape of the transverse pronotal band in that it is narrow and pointed ventrally. The lateral portion of the transverse band (seen in lateral view) is wider in front of the pronotal carina than behind it. In the remaining non-parasitic species of the *P. dominula* species group (*P. associus*, *P. dominula,* and *P. bucharensis*) the portion of the yellow band behind the carina is always wider. However, some extremely xanthic females of *P. nimpha* from western Asia also possess a very wide pronotal band. About 70% of females from western Asia have paired yellow drop-shaped spots on the mesoscutum. These spots are usually absent in European specimens. The visible part of the hypopygium (sternite VI) is usually black or partly reddish in *P. nimpha* and also in *P. associus*, rarely with a yellowish apical spot, while the hypopygium is entirely or predominantly yellow in *P. dominula* and *P. bucharensis*.

The latter character is used here for recognition of *P. nimpha* and *P. bucharensis* in eastern Turkey. This character is helpful in distinguishing xanthic *P. nimpha* females (i.e., with an all-yellow clypeus and temple), which are otherwise similar to *P. bucharensis*. Often only a combination of a several characters will ensure a correct identification of western Asian specimens.

The separation of *P. associus* and *P. nimpha* females can also be difficult, especially in areas where both species occur sympatrically (e.g. in western Croatia). The colour pattern of *P. associus* is diagnostic and exhibits little variation (based on specimens identified by barcoding): Transverse pronotal band wide laterally, separated from posterior band by 2-3 times the diameter of the anterior ocellus; mesoscutum with two large drop-shaped yellow spots. Despite significant variation, western Asian *P. nimpha* never show this combination of characters. The hypopygium colour is variable in both species but never all red in *P. nimpha* as it sometimes is in *P. associus* (one female from Israel).

Distribution. Europe, north to S Finland, Palaearctic Asia east to Mongolia, China, and Russian Far East.

Specimens examined. Europe: Germany, Italy (Alps), Bulgaria, Greece, France, Croatia, Portugal, Switzerland. Asia: Iraq, Turkey (Kars/Kagisman, Hakkari region, Denizli/Pamukkale, Antakya, Alanya, Marmaris, Diyarbakir).

Genetic results. Only specimens from Central Europe were examined genetically, except for one specimen from Greece. The species shows significant intraspecific genetic variation. It is possible that the examination of Asian species will yield unexpected results.

Polistes semenowi **Morawitz**

Figs 24, 57

Polistes semenowi Morawitz, 1889, Horae Entomol. Soc. Ross. 23: 552. – 3 female syntypes (ZISP, photo of 1 female examined by CvA who hereby designated it as lectotype), type locality: Copet-dag [Kopet Dag], S Turkmenistan. The illustrated female (labelled: “Copet-dag, 29-30.iv.[18]88, A. Semenov”, “K.F. Morawitza”, “*semenowi* F. Morawitz”) is the lectotype.

Polistes sulcifer Zimmermann, 1930, Mitt. Zool. Mus. Berlin 15: 610. Holotype male (MFNB, examined by CSE), type locality: Mendel-Penegal, Südtirol (N Italy). **Syn. n.**

Figure 57. *Polistes semenowi*. Lectotype female, habitus, lateral aspect, and labels. Photo: K. Samartsev.

Pseudopolistes sulcifer var. *similator* Zirngiebl, 1955, Mitt. Münchner Entomol. Ges. 44/45: 384. Holotype female (ZSM, examined by CvA and CSE), type locality: Ordubad [19]13, leg. Klar. **Syn. n.**

Sulcopolistes sulcifer auctt. (e.g., Guiglia 1972).

Remarks. The species was formerly treated as *P. sulcifer* by authors. See also comments under *P. austroccidentalis* for the nomenclature and taxonomy of this species.

Diagnosis. The species can only be recognized based on the shape of the mandible, clypeus, and the colour of male fore and mid coxae. The upper ridge of the mandible is markedly modified in the female and forms a triangle in dorsal view (weaker and more rounded in male). The recognition of males is more difficult because the upper ridge is sometimes only weakly curved and resembles that of *P. austroccidentalis*. The mandibles (frontal view) differ between both species in that the mandibular depression is narrower in *P. austroccidentalis* and with a wider upper mandibular ridge. Furthermore, the male fore coxa is almost always and the mid coxa usually marked with yellow as opposed to *P. austroccidentalis* where all coxae are black.

Life history. *Polistes semenowi* is a social parasite of *P. dominula* (see Cervo 2006, as *P. sulcifer*), in western Asia probably also of *P. bucharensis*.

Distribution. S and C Europe, north to Germany (Hesse, one record from 1908; Tischendorf et al. 2015 as *P. sulcifer*), east to Central Asia, not recorded from Spain and Portugal. One female in coll. MFNB labelled „Egypt, Ehrenberg leg"] has more yellow coloured hind coxa than usual. Its origin is doubtful as is that of an *atrimandibularis* specimen with the same data (see discussion under that species). No other specimens from North Africa have been examined by the authors. Males are sometimes found at higher altitudes (e.g., five males from Italy, Dolomiti, Rif. Coldai at 2150 m; 2 males from Greece, Mt. Olympus at 2200-2500 m, in coll. CSE).

Specimens examined. Europe: France, Croatia, Italy (Alps, Abruzzi, Calabria, Sicily), Greece, Macedonia, Montenegro, Serbia, Switzerland. Asia: Azerbaijan, Turkey (Uludağ, Bursa, Van), Syria, Egypt, Turkmenistan.

Genetic data. Barcoded specimens from south-central Europe showed little genetic variation.

Other subgenera

The following species are only discussed briefly, because they were either introduced only recently or they occur near the southern border of the study area. For further information on the nomenclature of these species see Carpenter (1996). For identification of the subgenus *Gyrostoma* and other Asian species see Richards (1984a) and Tan et al. (2014).

Subgenus *Aphanilopterus* Meunier, 1888

Polistes major Palisot de Beauvois

Polistes major Palisot de Beauvois, 1818, Insect. Recueill. Afrique Amérique, livr. 12: 206.

Distribution. The nominate subspecies of *Polistes major* has been found in northern Spain (Castro et al. 2013). The species ranges from the southern U.S.A. to Brazil and Peru, including several Caribbean islands (Carpenter 1996).

Subgenus *Gyrostoma* Kirby, 1828

Polistes olivaceus (DeGeer)

Vespa olivacea DeGeer, 1773, Mem. Hist. Insect. 3: 582, pl. 29 fig. 9.

Distribution. The species is recorded from E Africa, S Asia and Australia (Carpenter 1996). Richards (1984b) mentions records from Oman.

Polistes wattii Cameron

Polistes wattii Cameron, 1900, Ann. Mag. Nat. Hist. (7) 6: 416.

Distribution. The species is recorded from SW and S Asia (Arabian Peninsula, Iran, India, and S China) according to Richards (1984b) and Carpenter (1996).

Results of phylogenetic analysis and discussion

The phylogenetic analysis based on Bayesian inference resulted in a split of the included *Polistes* species into two major clades, with a posterior probability support value of 0.84 for the *P. gallicus* group (including *P. foederatus*, *P. bischoffi*, *P. gallicus*, *P. biglumis*, *P. albellus*, and *P. mongolicus*), and with a branch support of 1.0 for the *P. dominula* species group (including *P. dominula*, *P. bucharensis*, *P. austroccidentalis*, *P. atrimandibularis*, *P. semenowi*, *P. maroccanus*, *P. nimpha*, and *P. associus*) (Fig. 58). *Polistes dominula* is represented by two clades with *P. bucharensis* in between, illustrating the need for a closer examination of the status of the disjunct *dominula* clades. The sister group of the *dominula*/*bucharensis* clade is composed of a well-supported (pp = 1.0) clade consisting of the four social parasite species *P. atrimandibularis*, *P. austroccidentalis*, *P. maroccanus, and P. semenowi* and (Fig. 58), supporting the notion of a single origin of their biology. Within the *P. gallicus* species group there is some support for a clade composed of *P. foederatus*, *bischoffi*, *gallicus*, and *biglumis* (Fig. 58).

These results concur with an earlier analysis of a mitochondrial gene fragment (16S ribosomal RNA) by Choudhary et al. (1994). In their analysis, the three examined social parasites form a monophyletic group that is nested within other European *Polistes*. Unlike their study, where the parasitic clade came out as the sister group to *dominula+nimpha*, our analysis yielded the *dominula*/*bucharensis* clade as the sister group, albeit with low branch support (0.63, Fig. 58). *Polistes nimpha*, on the other hand, came out as the sister group to the clade comprising of *P. dominula*/*bucharensis* and the social parasites. This sister group relationship is supported by a robust branch support of 1.0 (Fig. 58). Based on the results of the present analysis, the following species groups are proposed within the subgenus *Polistes*.

The most important change affected the two species *P. associus* and *P. biglumis*. *Polistes associus* was formerly treated as a member of the *P. gallicus* species group (= subgenus *Leptopolistes* sensu Guiglia 1972) because of the narrowed temples of the male – a typical

Table 3. Species and species groups of *Polistes* based on the present study and compared to Guiglia (1972). (Sg. = subgenus, * social parasite)

Species	Proposed species group	Guiglia (1972)	Transferred to
albellus	*gallicus* group	(Sg. *Leptopolistes*)	
associus	*dominula* group	Sg. *Leptopolistes*	*dominula* group
*atrimandibularis**	*dominula* group	Genus *Sulcopolistes**	
*austroccidentalis**	*dominula* group	Genus *Sulcopolistes* (as *S. semenowi*)	
biglumis	*gallicus* group	Sg. *Polistes*	*gallicus* group
bischoffi	*gallicus* group	Sg. *Leptopolistes*	
bucharensis	*dominula* group	(Sg. *Polistes*)	
dominula	*dominula* group	Sg. *Polistes* (as *P. gallicus*)	
foederatus	*gallicus* group	Sg. *Leptopolistes*	
gallicus	*gallicus* group	Sg. *Leptopolistes* (as *P. omissus*)	
*maroccanus**	*dominula* group		
mongolicus	*gallicus* group	(Sg. *Leptopolistes*)	
nimpha	*dominula* group	Sg. *Polistes*	
*semenowi**	*dominula* group	Genus *Sulcopolistes* (as *S. sulcifer*)	

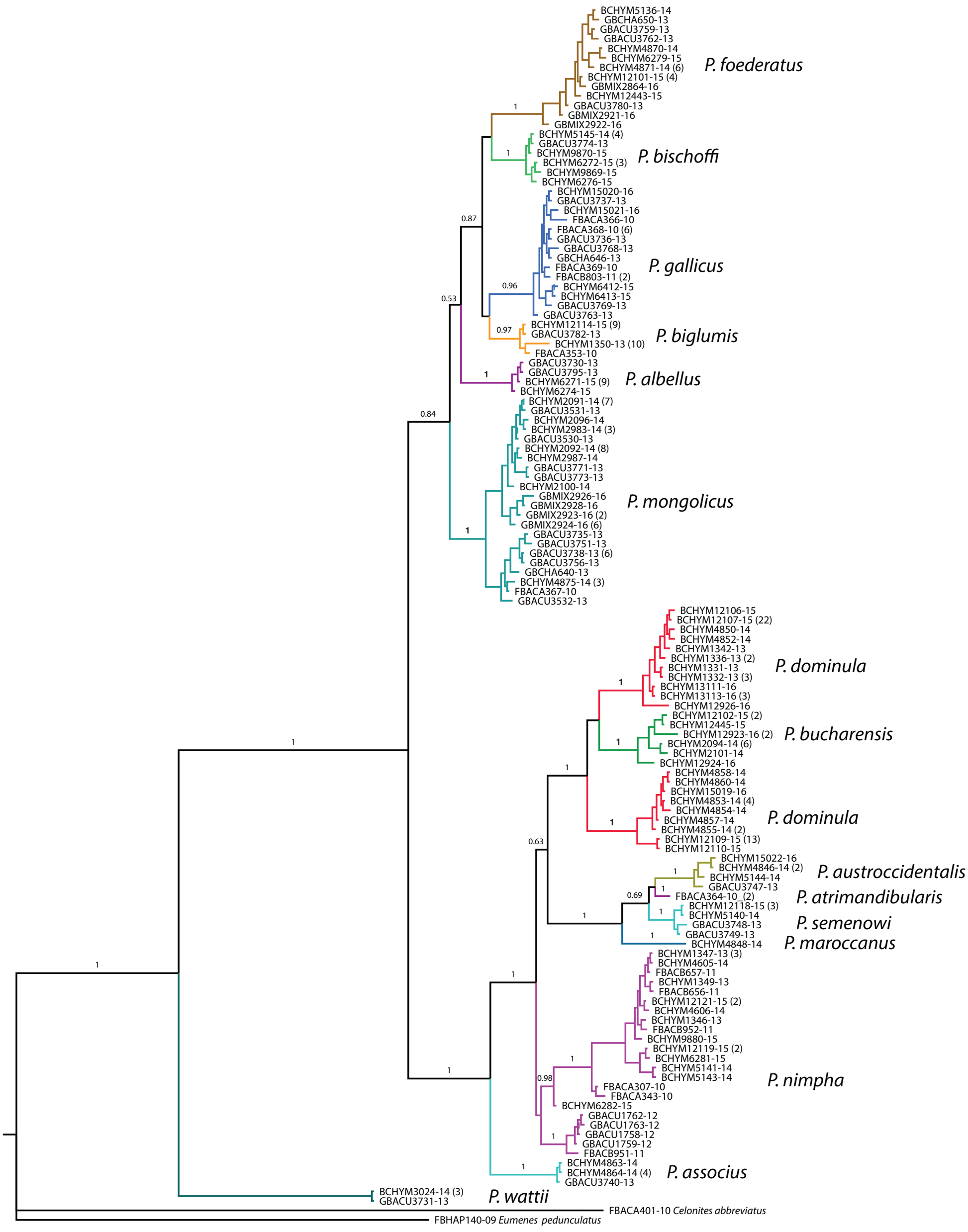


Figure 58. Phylogenetic tree resulting from Bayesian analysis of COI sequence data. Number in brackets after terminal branch labels (Process ID) indicate number of haplotype sequences. Numbers on branches denote posterior probability values (omitted for branches within species).

character of this subgenus, according to former authors. However, females of *P. associus* are morphologically and genetically close to *P. dominula*/*P. bucharensis* and *P. nimpha*, and can easily be confused with the latter species, providing support for placing the species in the *dominula* species group.

Likewise, *P. biglumis* was traditionally treated as a member of the *P. dominula* species group (= subgenus *Polistes* sensu Guiglia 1972), based on the broad, convex temples of the males. The female, however, is very similar to *P. albellus*, and the species has close relationships to the *P. gallicus* species group (= subgenus *Leptopolistes* sensu Guiglia 1972).

Despite the comparatively limited informative value of a single mitochondrial gene region like the 658bp COI barcode fragment, it still provides insights into phylogenetic relationships within the group and the phylogenetic relationships resulting from the analysis are largely in agreement with inferred by other lines of evidence. A more comprehensive analysis of *Polistes* including additional genetic markers, in particular of nuclear genes (see Neumeyer et. al. 2014), should be employed for evaluating and scrutinising the results of the present study.

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Supplementary material 1

List of voucher specimens

Authors: Christian Schmid-Egger, Kees van Achterberg, Rainer Neumeyer, Jérôme Morinière, Stefan Schmidt

Data type: Microsoft Excel Worksheet (.xlsx)

Explanation note: specimens date.

Link: https://doi.org/10.3897/zookeys.713.11335.suppl1

Supplementary material 2

NJ tree

Authors: Christian Schmid-Egger, Kees van Achterberg, Rainer Neumeyer, Jérôme Morinière, Stefan Schmidt

Data type: Adobe Acrobat Document (.pdf)

Explanation note: phylogenic date.

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RESEARCH ARTICLE

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The real taxonomic identity of *Trigona latitarsis* Friese, 1900, with notes on type specimens (Hymenoptera, Apidae)

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Abstract

The taxonomic history of *Trigona latitarsis* Friese, 1900 and its clarification based on the observation of the types and literature data are treated in this study. The paper discusses the validity of the previously proposed lectotype, deposited in the ZMB (Berlin, Germany). Based on the type series deposited in HNHM (Budapest, Hungary) as well as the original description, a new lectotype and 15 paralectotypes from Amazon forest (São Paulo de Olivença, Amazonas) are designated. Data on the geographic distribution of *Scaura latitarsis* (Friese, 1900) are provided.

Resumo

A história taxonômica de *Trigona latitarsis* Friese, 1900 é tratada nesse estudo, bem como esclarecimentos com base na observação dos tipos e em dados de literatura. É discutida a validade do lectótipo proposto anteriormente e depositado na ZMB (Berlim, Alemanha). Com base na série-tipo depositada no HNHM (Budapeste, Hungria), conforme descrição original, lectótipo e paralectótipos da floresta Amazônica (São Paulo de Olivença, Amazonas) são designados. Dados sobre a distribuição geográfica de *Scaura latitarsis* (Friese, 1900) são também fornecidos.

Keywords
Identification, lectotype, Meliponini, morphology, stingless bee, taxonomy

Introduction

The genus *Scaura* Schwarz, 1938 is composed of small and dark bees, with unusually enlarged hind basitarsus (wide as or wider than the hind tibia). The genal area is narrower than the compound eye in profile view and the malar space shorter than the diameter of the flagellum (Silveira et al. 2002). The distribution of the genus is broadly Neotropical, from Mexico to southern Brazil (Camargo and Pedro 2013).

Scaura was first described by Schwarz (1938) as a subgenus of *Trigona* Jurine, 1807, under the name *Trigona* (*Scaura*) *latitarsis* Friese, 1900, based on the enlarged hind basitarsus as the main diagnostic characteristic. Later, Schwarz (1948) included *Melipona longula* Lepeletier, 1836, in this subgenus, considering it to have two subspecies (originally treated as varieties): *T.* (*S.*) *longula longula* and *T.* (*S.*) *longula tenuis* (Ducke, 1916), based on width of the hind basitarsus, the edentate mandible and the rather triangular hind tibiae. Currently, these three forms are considered distinct species (Michener 1990, Camargo and Pedro 2013, Oliveira 2016), included in *Scaura* as an individualized genus apart from *Trigona*. This interpretation was initiated by Moure (1944) when he included three species of *Scaura* in a list of Peruvian species. Additional recognition characters of *Scaura* were provided by Moure (1951) who highlighted the absence of yellow spots on body, the malar space narrower than the flagellum diameter, the forewing with acute angle in submarginal cell and the abdomen narrower than the thorax.

In the original description of *Trigona latitarsis*, Friese (1900) described the female and the male, citing three workers and three males among the type material from Brazil (São Paulo) and Suriname. However, he does not identify the institution in which they were deposited, but he included several males from São Paulo among the syntypes that are deposited in the Hungarian Natural History Museum (HNHM - Budapest, Hungary). The specimen designated by Melo and Costa (2004) as lecotype of *Trigona latitarsis* is a worker from Jundiaí, São Paulo, which is deposited in the Museum für Naturkunde Berlin (ZMB, Berlin, Germany).

Based on some doubts arising from the study of the type material of *Trigona latitarsis*, the aim of the present study is to clarify some issues related to the taxonomic identity of *Scaura latitarsis*, based on the information available in the original description and of records species occurrence. The study also discusses the validity of the lectotype designated by Melo and Costa (2004), adds information on the syntypes, the type locality, morphological characters of the type series specimen, its taxonomic identify and, finally, the designation of a specimen of the type series as the new lectotype.

Materials and methods

The type material designated by Friese was studied by the second author of this study, during her trip to the HNHM in 2014. All the specimens deposited in those collections which were identified and labeled by Friese as *Trigona latitarsis* were studied. Specimens found and identified as belonging to the type series of *Trigona latitarsis* were borrowed and brought to Laboratório de Bionomia, Biogeografia e Sistemática de Insetos (BIOSIS-UFBA, Salvador, Bahia, Brazil). There, they were studied, measured, and photographed with the use of a stereoscopic microscope Leica M165C, coupled with a digital camera Leica DFC295 and containing the Application Suite V4.1 Interactive Measurements, Montage program.

The material designated by Melo and Costa (2004) as lectotype of *Trigona latitarsis* (Figs 1–4) was loaned from Museum für Naturkunde Berlin (**ZMB,** Berlin, Germany) to the Laboratório de Hymenoptera, Instituto Nacional de Pesquisas da Amazônia (**INPA**, Manaus, Amazonas, Brazil), where it was studied with the use of the same stereomicroscope described above.

In the diagnosis below, the symbol "♀" refers to worker, "♂" refers to male, "**Q**" to queen, "**S**" to sterna and "**T**" to terga.

Taxonomic characterization

Scaura latitarsis (Friese, 1900)

Figs 5–26

Trigona latitarsis Friese, 1900: 388. Lectotype male (presently designated). Label data: written with black ink: "Brasil, S. Paulo, 631/156".

Melipona crassipes tenuis Ducke, 1916: 46, 47; Ducke, 1925: 342, 368 [taxonomic characters, geographic records]

Scaura crassipes tenuis; Moure 1944: 28, 29 [list].

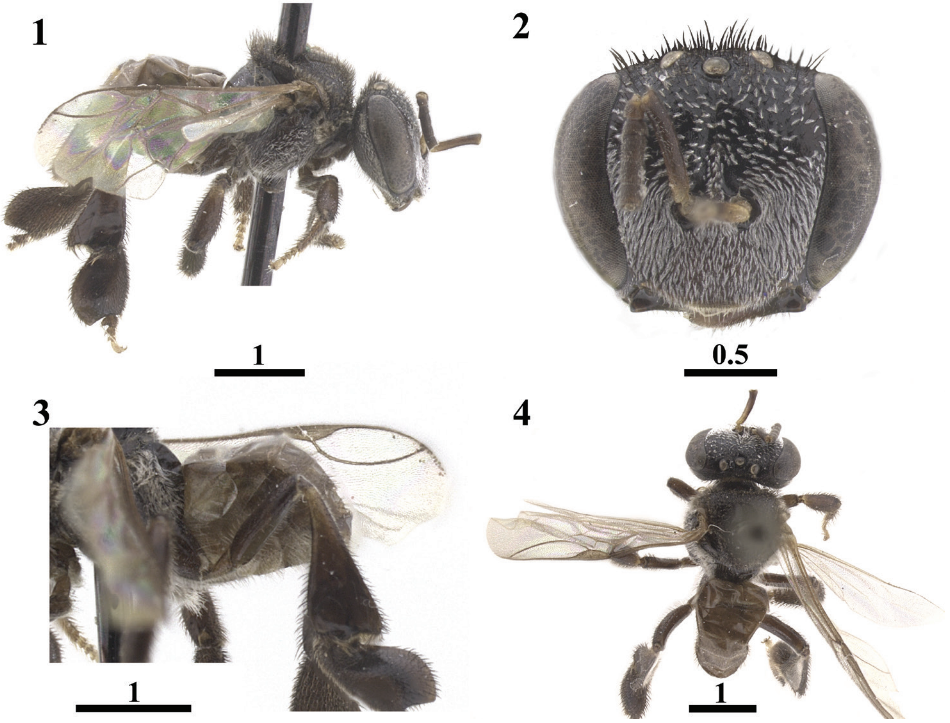
Trigona (*Scaura*) *longula tenuis*; Schwarz 1948: 489, 499, 500 [taxonomic characters, diagnosis, key, geographic records].

Trigona (*Scaura*) *tenuis*; Wille and Michener 1973: 12.

Plebeia (*Scaura*) *tenuis*; Michener 1990:114 [systematics, taxonomic characters, key]; Nates-Parra 2001: 239 [geographic records]; Smith-Pardo, 2003: 388 [list].

Scaura tenuis; Silveira et al. 2002: 91 [list, geographic records]; Camargo and Pedro 2002: 108 [taxonomic characters]; Camargo and Pedro 2013 [online catalog]; Oliveira et al. 2013: 163–167, 228. figs 297–313 [taxonomic characters, geographic records, key]; Oliveira 2016 [online catalog]. **Syn. n.**

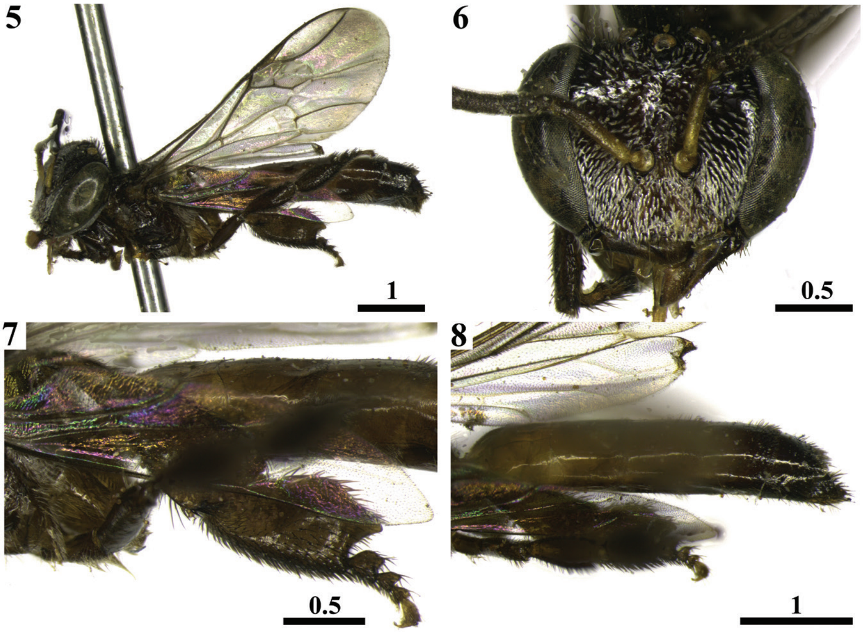
Diagnosis. (♀) Scape almost entirely yellow, with a dark spot on the apical third of dorsal surface (Fig. 6); forehead setae blackish and hairs whitish mixed; whitish simple



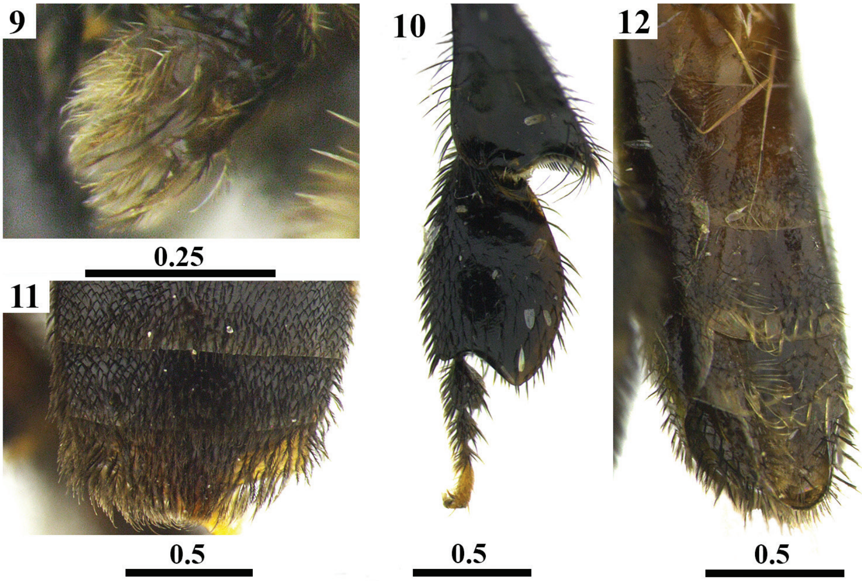
Figures 1–4. Lectotype of *Trigona latitarsis* Friese, 1900, designated by Melo and Costa (2004) deposited at the ZMB, invalidated in this study. Lateral view **1** Frontal view of head **2** Lateral view of hind leg and metasoma **3** Dorsal view **4** Scale bars in millimeters.

and ramified hairs on mesosoma; blackish setae intercalating the ramified whitish setae on pronotal lobes (Fig. 9); apex of the posterior border of mesothoracic basitarsus sharp (Figs 5, 10); metasoma elongated; blackish setae on T4 to T6 and whitish on sterna (Figs 11, 12). (♂) Ocellocular distance similar in length to the diameter of the lateral ocellus; blackish setae on vertex; whitish hairs on mesosome, blackish setae in terga T4 to T6 and whitish on sterna; valves with rounded base and tapering gradually to apex; posterior groove of spathe deep and sharp in dorsal view (Fig. 19); gonocoxite similar to an equilateral triangle; setae short and thick, restricted to the apical half of inner face of gonostile and the fourth apical of outer face. (Q) Setae of mandibles about half the mandible length; propodeum slightly concave in lateral view; metathoracic basitarsus about 5.5× longer than broad; junction area of fifth sternum apical lobes straight in ventral view; separation of these lobes a little bit pronounced.

Worker redescription. ***Paralectotype worker*** **(Figs 5–12).** *Color*: Integument predominantly brown-blackish. Clypeus dark brown, labrum yellowish brown. Mandibles brown, except the yellow apical 1/4. Mandibular condyles more darkened. Scape yellowish, with a brown spot in the apical third of dorsal surface; flagellum brown. Pronotal lobe yellowish-brown. Legs light brown, coxae slightly lighter than the other segments. Femora, tibiae and basitarsus slightly darkened on sides. Two last prothoracic tarsomeres yellowish-pale. Last segments of meso and metathoracic legs yellowish-



Figures 5–8. Paralectotype worker of *Trigona latitarsis* Friese, 1900 deposited at the Entomological Collection of the HNHM. Lateral view **5** Frontal view of head **6** Lateral view of hind leg **7** Lateral view of metasoma **8** Scale bars in millimeters.



Figures 9–12. Details of *Trigona latitarsis* Friese, 1900 workers of the additional material examined from Amazonas State. Blackish setae among the ramified whitish setae on pronotal lobe **9** Apex of the posterior border of mesothoracic basitarsus sharp **10** Blackish setae on T4 to T6 **11** Whitish setae on sterna **12** Scales in millimeters.

pale. Tegulae, wing venation and pterostigma dark brown. Wing membrane uniformly slightly smoky, with iridescent sheen. Apical half of T1 to T3 brown amber, T4-T6 more darkened towards the apex, tending to brown. S1 to S4 yellowish-brown, the other sterna slightly darkened, tending to brown.

Pubescence: malar area covered with simple white setae, fairly dense, but extremely short. Face with relatively sparse setae, branched on base, decumbent at lower clypeus and parocular area, and semi-erect on forehead; setae of upper end of forehead with most compact branches. Erect setae intercalating the branched ones on face, whitish in the lower half and darkened a little above half; longest bristles on clypeus (0.1 mm) and vertex (0.2 mm), and shortest on middle and lower parocular areas (0.05 mm). Whitish setae on scape, with 0.025 mm. Metathoracic wings with five hamuli. Pro and mesothoracic trochanter with whitish simple hair on the underside; similar but more sparse on the metathoracic. Setae of legs darker from the apical third of femurs to the apex, also gradually longer and thicker towards of the legs apex. Disk of mesoscutum with erect and darkened setae, relatively long (0.25 mm) and thick, these even longer in posterior board of scutellum (0.3mm). Mesepisternum with simple, whitish and relatively long hairs (0.24 mm), interspersing the whitish and branched (0.12 mm). T1 and T2 practically glabrous with a narrow strip of lower and pale setae on their board, with some very short setae on the apical half of sides of terga, setae gradually thicker and darkened, from the widest apical band of T3 toward of the metasoma apex. Apical band especially wider in the middle region of terga; T6 with some simple setae interspersing branched setae; setae on T3 with 0.07 mm; T4 with 0.13 mm; T5 with 0.17 mm and T6 with 0.18 mm. S1–S6 with whitish setae on their apical bands, about 0.13 mm length, the last fully setaceous.

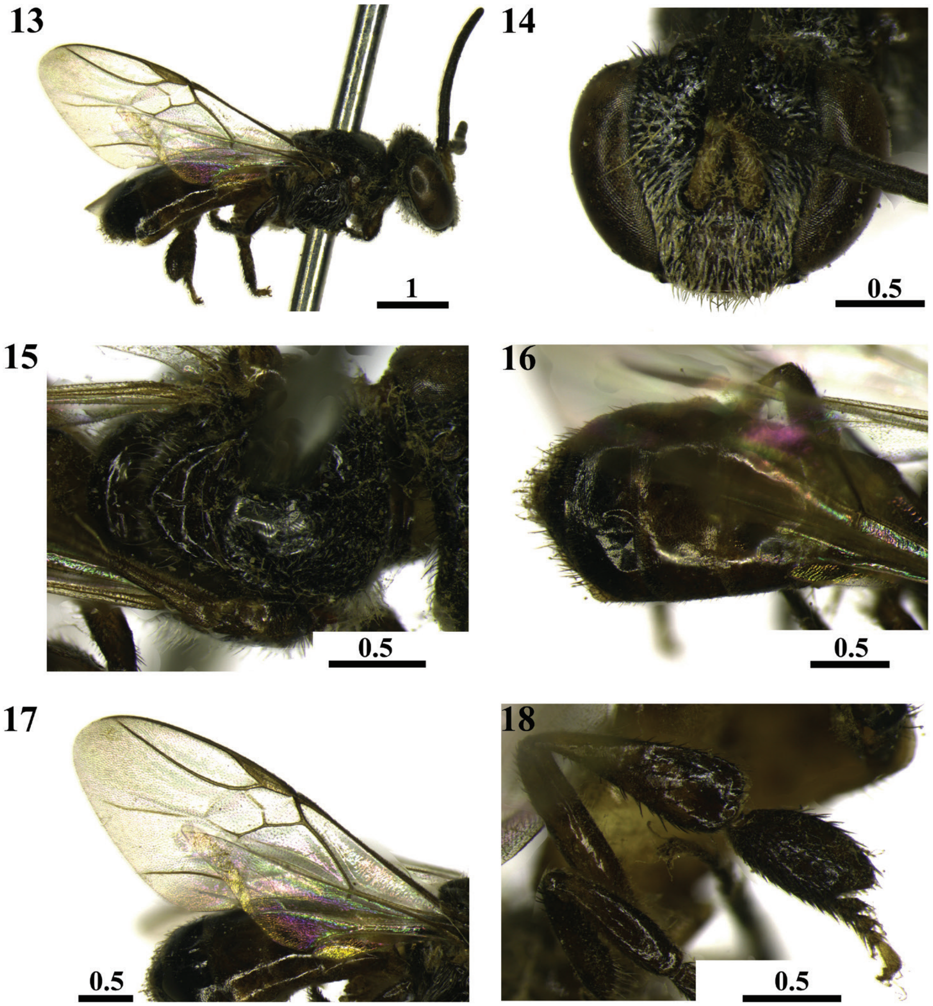
Integument surface: Fully smooth and shiny with only piliferous punctuation. Vertex distinctly higher at ocelli level.

Measurements (mm): Body length: 6.0. Head width: 2. Head approximately 1.5× wider than long (2.0: 1.34). Distance between the medium ocelli and the compound eye: 0.43; interorbital distances maximum and minimum (1.3: 0.91). Clypeus 1.7× wider than long (0.85: 0.48). Scape approximately 6× longer than its median width (0.61: 0.1). Pedicel about as long as wide (0.097: 0.096). Malar area: 0.05. Mesothoracic wing length of: 4.7. Metasoma elongated.

Specimen condition: very dirty, the left prothoracic tibia and tarsus, right prothoracic distitarsus, right mesothoracic tibia, tarsus and right metathoracic leg missing.

Label data: “Brasilia” [= Brasil], “631”, “365”, “Trigona latitarsis Friese, 1900” [written by Friese with black ink].

Description. ***Male*** **(lectotype) (Figs 13–18, 26).** *Color*: Integument predominantly brown-blackish. Clypeus brownish, labrum and apical third of mandible yellowish. Scape yellow with a brown spot in apical third of dorsal surface. Pedicel brown. Flagellum dark brown. Pronotal lobe translucid brown. Legs brown-yellow with brown darkened spots on the apical half of femurs, basitarsus more darkened than rest of legs; metathoracic tibia with large yellowish areas, with 1/5 apical and metathoracic board more darkened. The last tarsomeres yellow. Tegulae, alar venation and pterostigma

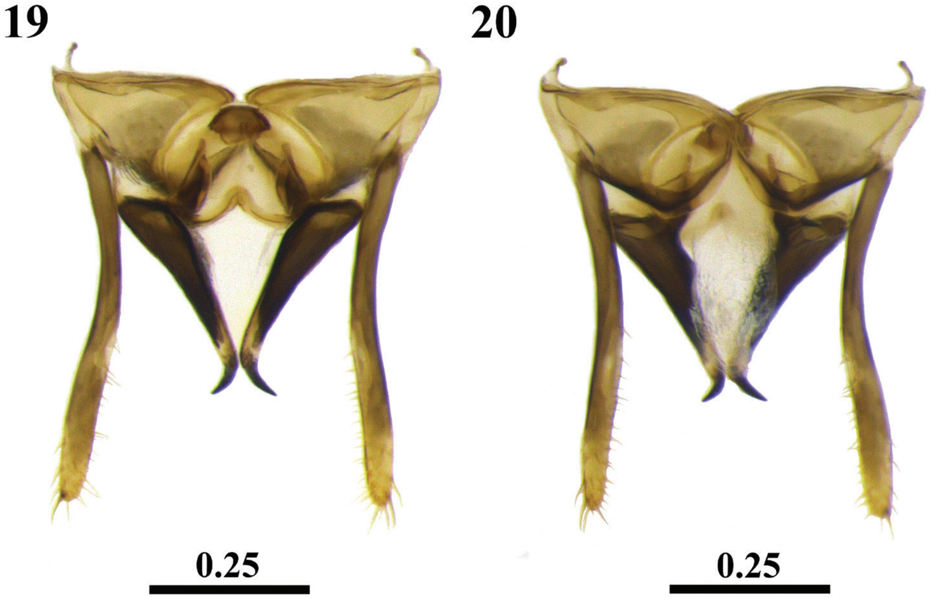


Figures 13–18. Lectotype male of *Trigona latitarsis* Friese, 1900 deposited at the Entomological Collection of the HNHM. Lateral view (**13**) Frontal view of head (**14**) Dorsal view of mesosoma (**15**) Dorsal view of metasoma (**16**) Forewing (**17**) Lateral view of hind leg (**18**). Scales in millimeters.

brownish. Wings membrane uniformly slightly smoky, with iridescent sheen. T1 yellowish-brown, T2-T4 brown; T5 to T7 more darkened than the others. Sterna yellowish, the last two brownish.

Integument suface: similar to that of worker.

Pubescence: similar to the worker, except for the following characters: plumose pilosity densest on face; thinner and shorter setae on mesosome; setae of mesoscutum disc notably shorter, sparser and thinner, with few interspersed darkened setae; setae of the scutellum notably thinner and sparse, fully whitish; band of tiny setae on posterior board of T1 to T3 pale yellow; erect setae longer, thick and darkened from T4 to the tip of metasoma; erect setae on the sides of terga.



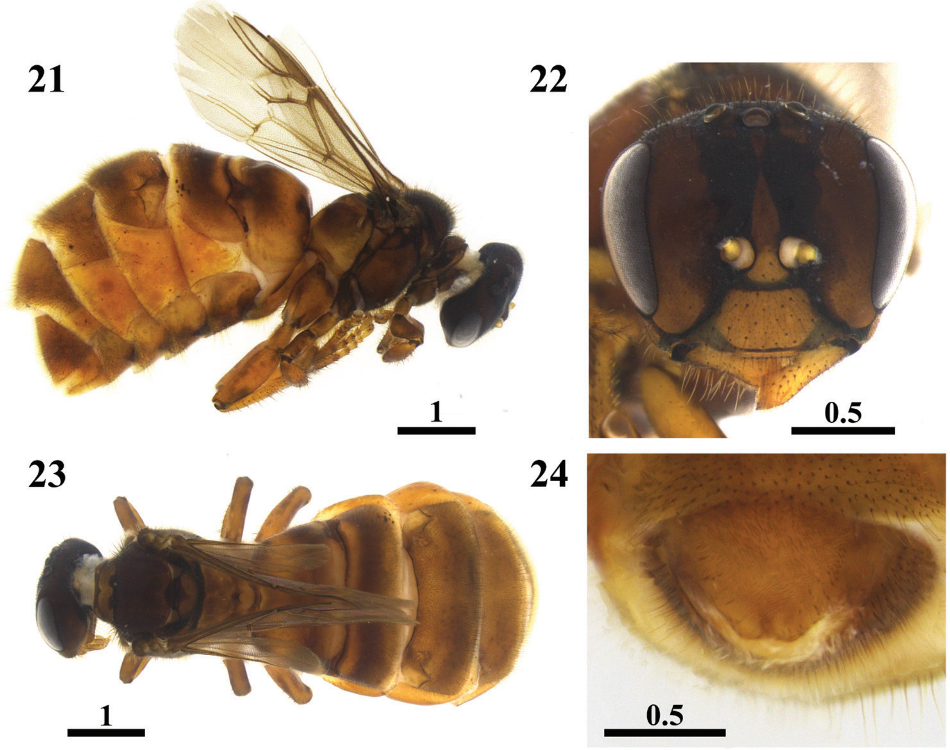
Figures 19, 20. Male genital capsule of *Scaura latitarsis* (Friese, 1900). Dorsal view (**19**) Ventral view (**20**). Scales in millimeters.

Measurements (mm): Body length: 5.00. Head width: 1.8. Head approximately 1.2× wider than long (1.8: 1.4). Distance between the compound eye and medium ocelli 0.5. Interorbital distance maximum and minimum (1.5: 0.7). Clypeus 1.6× wider than long (0.73: 0.45). Scape approximately 4× longer than its median width (0.56: 0.14). Pedicel 1.1× wider than long (0.17: 0.15). Malar area with 0.05. Mesothoracic wing length: 4.3. Metathoracic tibia 3.5× longer than wide (1.4: 0.4). Metathoracic basitarsus 2.1× longer than wide (0.84: 0.4). Metasoma elongated as the worker one.

Lectotype conditions: quite dirty, the left prothoracic leg and right metathoracic tibia missing.

Label data: written with black ink: “Brasil, S. Paulo”, “631/156”.

Queen. Physogastric queen (Figs 21–24). *Color*: Integument predominantly brown yellowish. Clypeus yellowish brown with outlines margin darkened. Labrum and mandibles yellowish brown. Mandibular condyles blackened. Antennae yellowish. Scape yellowish brown. Pronotal lobes blackish brown. Legs brown yellowish. Upper surface of femurs slightly darkened. Apical third of the lower surface of femurs blackened. Basal and apical margin of tibiae blackish. Metathoracic tibia with blackish spot on external face next to the posterior border. Tarsus yellow with basal edges blackened. Tegulae, wing venation and pterostigma dark brown. Wing membrane hyaline. Apical half of T1 and T2 dark brown. T3 with the apical half brown. T4–T6 brown yellowish. S1–S4 brown with yellowish sides. S5 brown in lighter shade than the other sterna.



Figures 21–24. Physogastric queen of *Scaura latitarsis* (Friese, 1900). Lateral view (**21**) Frontal view of head (**22**) Dorsal view (**23**) Ventral view of fifth sterna (**24**). Scales in millimeters.

Pubescence: malar area with few whitish and short setae. Simple and short setae on upper half of head (0.05 mm). Long, thick and semi-decumbent setae on clypeus and labrum interspersing the simple, thin, and dark brown, the longer on apical half of clypeus (0.14 mm). Greater abundance of setae near the apex of mesothoracic wings, the metathoracic with 5 hamuli. Trochanters with simple whitish hairs which are more abundant on lower face. Basal third of prothoracic femurs and basal half of the mesothoracic with simple whitish hairs on the underside. Metathoracic femurs with longer setae on basal and latero-anterior range to the apical region. Metathoracic tibiae and basitarsus with yellowish setae with brownish sheen; on tibiae, setae longer in the posterior border. Disk mesoscutum with sparse and long blackish simple setae (0.19 mm), interspersing the very abundant whitish setae, these later with a third of the length of the largest blackish setae. Mesepisternum (0.20 mm) and metepisternum (0.12 mm) with only simple hairs. Anterior margin of T1 with simple sparse whitish hair. Apical margins of terga with blackish, short and less abundant setae throughout their length. Apical half of T2–T5 with dark setae. T6 with blackish setae throughout its length. Pubescence on T3 with 0.19 mm; on T4 with 0.23 mm; T5 with 0.25 mm and T6 with 0.23 mm. Apical half of S1–S4 with simple and whitish setae. S5 with setae in its entire length.

Integument surface: Head, meso and metasoma entirely smooth and shiny. Vertex slightly elevated. Tibiae and basitarsus smooth between microtrichia.

Measurements (mm): Body length: 6.15. Head width: 1.57. Head about 1.28× wider than long (1.57: 1.22). Distance between medium ocelli and the compound eye: 0.43; interorbital distances maximum and minimum (1.15: 1.07). Clypeus 2.38× wider than long (0.81: 0.34). Malar area 0.14. Length of metathoracic coxae, trochanters, femurs, tibiae and basitarsus 0.66: 0.41: 1.15: 1.47: 0.65, respectively. Metathoracic tibiae 5× longer than wide (1.47: 0.29). Metathoracic basitarsus 5.4× longer than wide (0.65: 0.12).

Specimen condition: good, with a loose antenna preserved in alcohol.

Label data: "*Scaura tenuis*, Nova Xavantina MT – 9/12, Rainha F., Mateus leg", "Nova Xavantina, Nov/2012", "Rainha *Scaura tenuis*".

Discussion

A male deposited in the HNHM is designated as the lectotype, which has a label with the following information: "Brasil, S. Paulo", "631/156".

A total of 15 paralectotypes (13 males and 2 worker) of *Trigona latitarsis* Friese, 1900 is also deposited in HNHM (drawer 78/47), which were studied, validated, and labeled by the second author (Fig. 25): five males, all with labels printed with the name "Brasilia" (corresponding to Brazil), and another label with the number "631/156" handwritten (one specimen also has a label written in black ink with Friese's handwriting "*Trigona latitarsis* Friese, 1900"); six males with only a printed label with "Brasilia"; two males with a label handwritten in black ink, with the names "Brasil, São Paulo", also with another handwritten label with the number "631/156"; a worker with a handwritten label with the word "Brasil", and another label handwritten and numbered "631/365"; a worker with a printed label in which is written "Brasil" and a handwritten label with the numbers "631/365". Although the majority of syntypes of *Trigona latitarsis* deposited in the HNHM are males, and as Friese did not mention in the species description the females deposited at "Budapest collection", there are no doubts that these two workers also belong to type series of the *Trigona latitarsis*, once the data confer with males labels (especially the number 631, which seems to be the number of the locality of collection – in this case "São Paulo" – or collector, as observed in *Trigona latitarsis* labels and also in the types labels of other species described by Friese in 1900 – same paper), all specimens are of the same species and had been kept separate together with males. It also important to mention that the putative type specimens are the only specimens of this species deposited at the HNHM. Probably, because they were among a large number of males, which was not usual for species of Meliponini described by him, Friese did not notice the two female specimens (therefore these two female were also marked as paralectotypes). Specimens from Suriname, mentioned by Friese (1900), were not found in the collections of Berlin, Vienna, Munich, Paris, or Budapest, which are collections where most of Friese's types are deposited. All specimens in HNHM are labeled lectotype and paralectotypes by F. F. de Oliveira.

Figure 25. Syntypes of *Trigona latitarsis* Friese, 1900 deposited at the Entomological Collection of the HNHM.

Figures 26–28. Labels of type material deposited at the Entomological Collection of the HNHM. Lectotype of *Trigona latitarsis* Friese, 1900 (**26**) Lectotype of *Trigona heideri* Friese, 1900 (**27A, B**) Paralectotype *Trigona kohli* Friese, 1900 (**28**).

Material deposited in the ZMB: The worker, designated by Melo and Costa (2004) as lectotype of *Trigona latitarsis*, does not belong to the types series of this species according to our study, as this specimen has the following label data: “Brasil, Jundiahy, 1899, Schrottky”, “Zool. Mus. Berlin”, “latitarsis” [writing with blue ink pen], “LECTOTYPE, *Trigona latitarsis*, Friese, 1900, desig. Melo & Costa, 2004”. In his publication, Friese (1900) refers to Jundiaí (a town in São Paulo State, Brazil) in the description of other species, but not in the original description of *Trigona latitarsis*, where he cites only “São Paulo”. If the type locality was Jundiaí, he would have written the full reference of the label, as he did for the other species described in the same paper, also including the collector’s name (e.g. *Trigona schrottkyi* – page 386–387: “Brasilia: Jundiaby, 20. Oktoh. 1898 (Schrottky) und Saõ Paulo”). Unfortunately, all type series of *Melipona crassipes tenuis* Ducke, 1916 that should be in MPEG (Museu Paraense Emílio Goeldi, Pará, Brazil) are lost. Ducke (1916), in the description of this species, refers to specimens from Pará (Itaituba), Amazon (Rivers Javary and Japurá) and Mato Grosso (Tributaries of Tapajóz, collected by G. Kuhlmann). This fact had already been mentioned by Ducke (1916) when he described the geographical distribution of *Scaura latitarsis* (as "*Melipona latitarsis*"), where he clearly mentions that, according to Friese, this species occurs (or would be present) in São Paulo de Olivença (p. 28 lines 1 and 2). The true *Scaura latitarsis* has an elongated abdomen with abundant branched setae on the fifth and sixth terga. The species which has been interpreted as *S. latitarsis* by several authors for many years including Melo and Costa (2004) has short subtriangular abdomen (Oliveira et al. 2013), with few whitish hairs on the fifth and sixth terga.

It is noteworthy that all *Scaura* found in ZMB were examined and none of them correspond morphologically to *Scaura latitarsis*, nor do the label data correspond to those cited in the original description by Friese (1900). *Scaura latitarsis*: Melo & Costa, 2004 (unjustified lectotype).

Scaura latitarsis has been interpreted over the years by a number of different authors based on specimens from different regions of Brazil, including specimens from São Paulo State in southeastern Brazil, like the lectotype designated by Melo and Costa (2004). However, analyzing the older literature on this species and the type material of *Trigona latitarsis* (the newly designated lectotype and paralectotypes) deposited in HNHM and cited by Friese in the original description (16 specimens, two workers, and 14 male), we conclude that *Trigona latitarsis* does not correspond morphologically to what has traditionally been interpreted as *Scaura latitarsis*, and that these specimens that are traditionally (mis)interpreted as *S. latitarsis*. The species that have been traditionally (mis) interpreted as *S. latitarsis* (from São Paulo State and other regions of Brazil, as well as from Bolivia, Colombia, Guyana, Peru, Suriname and Venezuela), including the lectotype designated by Melo and Costa, corresponds to a new species (Nogueira *in litt.*).

Although the type material of *Melipona crassipes tenuis* Ducke, 1916 was not found, based on how species has been traditionally interpreted over the years by Ducke himself as *Trigona tenuis*, and also by Friese, Moure and Camargo, we conclude that the species described as *Melipona crassipes tenuis* Ducke, 1916 correspond to *Trigona latitarsis* Friese, 1900 (as junior synonyms) as interpreted in the current article. This conclusion is based on the type series of *T. latitarsis* and on the original description published by Ducke (1916), where he refers to the thin and elongated metasoma "Abdomen muito tenue" (p. 46), the main character that defines this species gaving rise its name, and which separates it from all the other species of *Scaura*.

The taxonomic confusion must have been generated by a misinterpretation of the type locality mentioned by Friese in the original description, cites only "Saõ Paulo", referring to São Paulo de Olivença city mentioned by Ducke (1916: 28), and not São Paulo State (southeastern Brazil). Given that *Scaura tenuis* does not occur in the state of São Paulo, but only in the Amazon region from Colombia, Ecuador, Peru, Suriname, French Guiana, Bolivia and Brazil (Fig. 29), we can conclude that the locality "Saõ Paulo" written on the label of some syntypes and mentioned by Friese in the original description refers to a small town in the Amazonas State, known as "São Paulo de Olivença", and not the state of São Paulo, as it has been interpreted since 1900 by different Meliponini taxonomists, including Silveira et al. (2002), Camargo and Pedro (2002), Melo and Costa (2004), Camargo and Pedro (2013) and Oliveira et al. (2013).

It is important to note that the Amazon locality now known as São Paulo de Olivença was founded as a village in 1689 (where a mission was carried out by Spanish missionaries), and, in this period, was known as "São Paulo Apóstolo". However, in 1708, this village came under the dominion of Portuguese missionaries and had its name changed to "São Paulo dos Cambebas". With its elevation to city status in 1817, it then received the name of "São Paulo de Olivença". With the creation of the Solimões district, on June 13, 1884, São Paulo de Olivença became a well-known city in the region, for having been chosen as the administrative center of this new district. Thus, in 1900, when the species in question was described, the village was known and visited by researchers and religious people (BVA 2014). This definition of the type locality as São Paulo de Olivença is a very important fact, and may modify the interpretation of many of syntypes of different species described by Friese.

Another important and relevant fact, which provides strong support for this new interpretation of *Scaura latitarsis*, can be seen in the original description, when Friese describes the male exemplar as having yellow scape (Fig. 14). This is not the case in those male specimens of the species from São Paulo State that have been interpreted as *T. latitarsis* (1/3 basal is yellowish brown). Even if the material type of Friese (syntypes) comprised of specimens of two species (that were being interpreted individually and *S. tenuis* and *S. latitarsis*), the information provided by the original description leaves no doubt about the validity of the taxon correspondence that had been interpreted as "*S. tenuis*" as being the same as "*T. latitarsis*", according to the original description (compared with syntypes studied here). Even if additional specimens belonging to the syntypes series be found in the future, and these prove that the "*T. latitarsis*" type series is composed of more than one species, it would not invalidate the new lectotype from Budapest (HNHM), as Friese clearly included males from Budapest Museum in the type series.

Friese emphasized in the original description that the yellow scape occurred only in the male. However, the ventral side of the scape is also yellow, in workers, although the color is restricted to the basal third. As the male scape is completely yellow with a strong tonality, it may have been this difference which Friese wished to emphasize in his description. Consequently, all specimens must have been collected in São Paulo de Olivença, although it was written on the label only "S. Paulo" (as noted in specimens deposited in HNHM). Additional important evidence comes from the fact that Friese does not mention Jundiaí in the description, as he does for other species described in the same article, and whose type material type was collected in Jundiaí (e.g. *Trigona schrottkyi* – pages 386–387 as mentioned previously). Therefore, the only encountered specimens found that we are confident belong to the type series are those of the HNHM, based on the description and data of the labels affixed to the specimens.

A similar case occurs with the Amazonian species *Trigona heideri* Friese, 1900 (= *Ptilotrigona lurida* (Smith, 1854)) described by Friese under the number 39, in the

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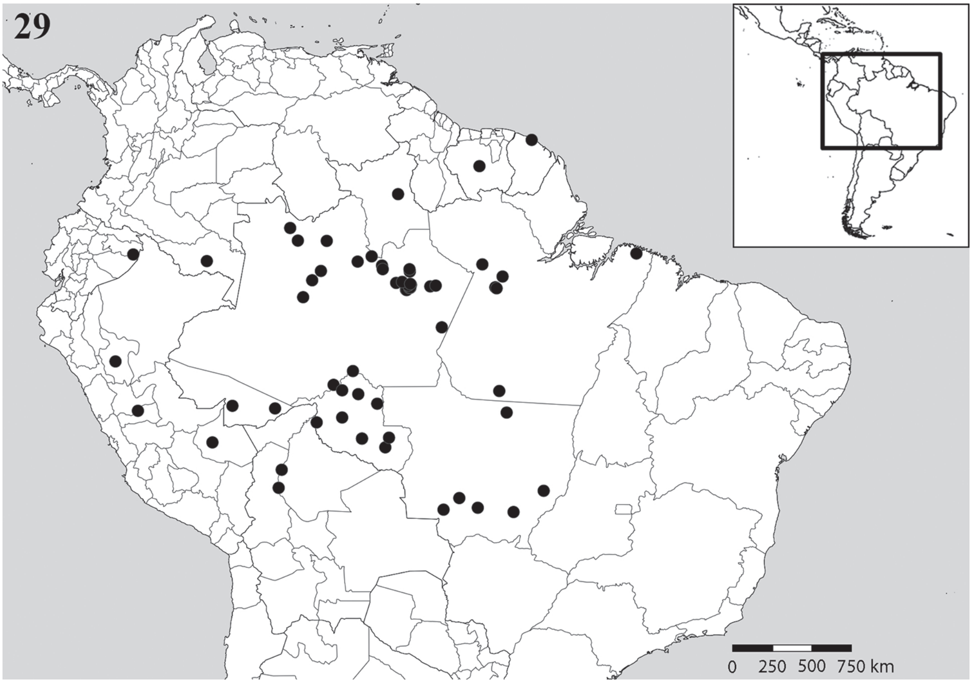

Figure 29. Map of South America showing the known geographic distribution records for *Scaura latitarsis* (Friese, 1900), based on the type material studied here, plus analysis of additional material analyzed from Amazon region and part of the Brazilian Cerrado; Bolivia: El Beni; Brazil: Acre, Amazonas, Pará, Rondônia, Roraima, Mato Grosso; Colombia: Amazonas, Meta; Ecuador: Napo; French Guyana: Cayenne; Peru: Huánuco, San Martín, Madre de Dios, Pasco; Suriname.

same paper (pages 389 - 390), one page after he described *Trigona latitarsis* Friese, 1900 (number 34, page 388). The species *Trigona heideri* was described by Friese based on 14 workers from Brazil (Brasilia: Para (Ducke, 29. Septbr. - 11. Novbr. 1899); S. Paulo, Obidos, Fonteboa, Amazonas), Columbia and Peru (Vilcanota), and the specimens were also deposited also at the HNHM.

Based on the type material from HNHM the specimen chosen by Claus Rasmussen (27.III.2006, *in litt.*), and designated as lectotype of *Trigona heideri* Friese, 1900, is a specimen from “S. Paulo”, and, like *Trigona latitarsis* Friese, 1900 has the same handwritten label in black ink (with the same handwriting) (Fig. 27A, B). For this species, Camargo and Pedro (2013) had also assumed that the type locality "S. Paulo" is in fact São Paulo de Olivença (Amazonas, Brazil), as this is an Amazonian species, and one that has never been recorded in São Paulo State (Southeastern Brazil).

An additional and similar case with *Trigona kohli* Friese, 1900 (=*Trigona pallens* (Fabricius, 1798)), described by Friese (1900) in the same article (number 29 on page 387), whose paralectotype was designated by Claus Rasmussen from the HNHM type series (Fig. 28). This too is an Amazonian species never recorded in São Paulo State (southeastern Brazil).

Carefully comparing the provenance labels of *Trigona latitarsis* Friese, 1900 (here designated as lectotype) (Fig. 26), *Trigona heideri* Friese, 1900 (lectotype designated by Claus Rasmussen) (Fig. 27 A, B) and *Trigona kohli* Friese, 1900 (paralectotype designated by Claus Rasmussen) (Fig. 28), it is easily seen that the three specimens have the same handwritten label in black ink, written by the same letter, which leads us to assume that they were collected in the same locality and had the labels written by hand by the same person. Also the number 631 appears on observed in the label of *Trigona latitarsis* (Fig. 26) and *Trigona heideri* (Fig. 27 A, B), which seems to be the some information about the locality of collection (in this case "São Paulo"), date, or collector.

Based on all information discussed here, we propose the male specimen in HMHN carrying the label written "S. Paulo" to be considered as lectotype of *Trigona latitarsis* Friese, 1900, replacing the specimen from Jundiaí designated by Melo and Costa (2004) (lectotype invalidated) and *Melipona crassipes tenuis* Ducke, 1916 and are to be considered a junior synonym of *Trigona latitarsis* Friese, 1900.

Summary of arguments for the current interpretation

1. Ducke (1916, p. 28, lines 1 and 2) received information from Friese himself and he said that *Trigona latitarsis* Friese, 1900 was from São Paulo de Olivença (a village in Amazon) and not from São Paulo State (Southeastern Brazil);
2. The label of *Trigona latitarsis* Friese, 1900 type material had written only the word São Paulo (village), as discussed in here. This is also the case for several other types from a number of different species described by Friese (1900), for which we had the opportunity of study the types in the HNHM;
3. The word "S. Paulo" without any other information ended up causing confusion as it referred to a village in Amazon and not to São Paulo State, which is what came to be assumed, even though this locality is situated in another, completely different, region;
4. There is no evidence from identification labels, or any other information associated with original description that proves that the specimen chosen by Melo and Costa (2004) could be, at least, be considered syntypes of *Trigona latitarsis* Friese, 1900;
5. Currently, the only material that can, for certain, be considered as syntypes of *Trigona latitarsis* Friese, 1900 is the material deposited at the HNHM and discussed here;
6. Even if the type series was composed of multiple species, as observed for several species described by Friese, and other material from Brazil or Surinam could be found in the future, and if it represented a different taxonomic entity (species), this does not invalidate the types from the Budapest Museum (HNHM), as once Friese clearly included these as syntypes of *Trigona latitarsis* Friese, 1900;
7. The same situation as occurred with *Trigona latitarsis* Friese, 1900, has also occurred with *Trigona heideri* Friese, 1900, where the same label with the same In-

dian ink handwriting was found. It is from this that Camargo and Pedro Pedro (2013) once again assumed that the locality to be São Paulo de Olivença and not São Paulo State (Southeastern Brazil);
8. This situation was also observed in *Trigona latitarsis* Friese, 1900, with the same label with the same label with identical handwriting in Indian ink was foud for *Trigona kohli* Friese, 1900 (=*Trigona pallens* (Fabricius, 1798)), which again is an purely Amazonian species and does not occur in São Paulo State (Southeastern Brazil);
9. In the same article win which Friese (1900) described *Trigona latitarsis* and several other species, the species from Jundiaí (Ex: *Trigona schrottkyi* Friese, 1900) has the following information on the label: Brasilia: Jundiaby [sic = Jundiaí, São Paulo], 20.X .1898, Schrottky leg., as observed in type. Why would Friese suppress this locality information only for *Trigona latitarsis*?
10. Some specimens of the syntype series from HNHM discussed in here have a Friese identification label, handwritten by that author (partially or totally with Indian ink), except that designated by Melo and Costa (2004).
11. Although the type material of *Scaura tenuis* was not found (is having been lost), in the original description by Ducke (1916), he refers to the slender metasome “Abdomen muito tenue” (p. 46), which supports the synonimization of *S. tenuis* under *S. latitarsis*.

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A new species of *Phrynopus* (Amphibia, Anura, Craugastoridae) from upper montane forests and high Andean grasslands of the Pui Pui Protected Forest in central Peru

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Abstract

We describe a new species of *Phrynopus* from the upper montane forests and high Andean grasslands (puna) of the Pui Pui Protected Forest and its close surroundings (Región Junín, central Peru) and compare it morphologically and genetically with other species of *Phrynopus*.

Phrynopus inti **sp. n.** is known from four localities outside and two localities inside the Pui Pui Protected Forest between 3350 and 3890 m a.s.l. Studied specimens of the new species are characterized by a snout-vent length of 27.2–35.2 mm in males (n = 6), and 40.4 mm in a single female, by having the skin on dorsum and flanks smooth with scattered tubercles, venter smooth, by lacking a tympanum, and males without vocal slits and nuptial pads. In life, the dorsum is pale grayish brown with or without dark brown blotches, or dorsum blackish brown with small yellow flecks, throat, chest and venter are pale grayish brown with salmon mottling, groin is pale grayish brown with salmon colored flecks, and the iris is golden orange with fine dark brown reticulations. The new species is morphologically most similar to *Phrynopus* *kauneorum* and *P. juninensis*. For the latter we describe the coloration in life for a specimen obtained at the type locality. A molecular phylogenetic analysis based on mitochondrial and nuclear DNA sequences inferred that the new species is most closely related to *Phrynopus kauneorum*, *P. miroslawae*, *P. tautzorum*, and an undescribed species distributed at high elevation in Región Pasco, central Peru.

Resumen

Describimos una nueva especie de *Phrynopus* de los bosques montanos altos y los pajonales altoandinos (Puna) del Bosque de Protección Pui Pui y sus áreas cercanas (Región de Junín, Perú central) y la comparamos morfológica y genéticamente con otras especies de *Phrynopus*. *Phrynopus inti* **sp. n.** es conocido de cuatro localidades fuera y dos localidades dentro del Bosque de Protección Pui Pui entre 3350 y 3890 m s.n.m. La nueva especie se caracteriza por tener una longitud hocico-cloaca de 27.2–35.2 mm en machos (n = 6) y 40.4 mm en una hembra, por tener la piel dorsal y los flancos lisos con tubérculos dispersos, el vientre liso, por carecer de un tímpano, y los machos carecer de hendiduras vocales y almohadillas nupciales. En vida, el dorso es marrón grisáceo pálido con o sin manchas marrón oscuro o el dorso es marrón oscuro con pequeñas manchas amarillas; la garganta, pecho y vientre son marrón grisáceo pálido con motas de color salmón, la ingle es marrón grisácea con manchas de color salmón y el iris es dorado naranja con finas reticulaciones marrón oscuro. La nueva especie es morfológicamente muy similar a *Phrynopus kauneorum* y *P. juninensis*. Para este último, describimos la coloración en vida de un espécimen obtenido en la localidad tipo. Un análisis filogenético molecular basado en secuencias de ADN mitocondrial y nuclear infirió que la nueva especie está más estrechamente relacionada con *Phrynopus kauneorum*, *P. miroslawae*, *P. tautzorum*, y una especie no descrita distribuida en zonas altoandinas de la Región Pasco, Perú central.

Keywords

Andes, montane forest, puna, frogs, DNA barcoding, molecular phylogeny, *Phrynopus inti,* new species

Palabras claves

Andes, bosque montano, puna, ranas, códigos de barras de ADN, filogenia molecular, *Phrynopus inti*, especie nueva

Introduction

The Pui Pui Protected Forest (Bosque de Protección Pui Pui, hereafter PPPF; Figs 1, 2) is located in the Selva Central of Peru and covers 60,000 hectares (30% montane forest, 70% puna habitats) between 1700 and 4500 m a.s.l. (SERNANP 2010). We surveyed the herpetofauna of the PPPF in upper montane forests and high Andean grasslands (puna) between 2012 and 2013 in order to document the amphibian and reptile species richness and to evaluate their conservation status. Among the new amphibians were five new species of *Pristimantis* (Craugastoridae Hedges, Duellman, and Heinicke, 2008) (*P. ashaninka* Lehr & Moravec, 2017; *P. attenboroughi* Lehr & von May, 2017; *P. boundes* Lehr, von May, Moravec, & Cusi, 2017; *P. humboldti* Lehr, von May, Moravec, & Cusi, 2017; and *P. puipui* Lehr, von May, Moravec, & Cusi, 2017) and a new species of *Phrynopus* Peters, 1873. A phylogenetic analysis allowed us to examine the relationships among species of *Phrynopus*, including the new species, and to justify our generic assignment. *Phrynopus* currently contains 34 species (AmphibiaWeb 2017) distributed

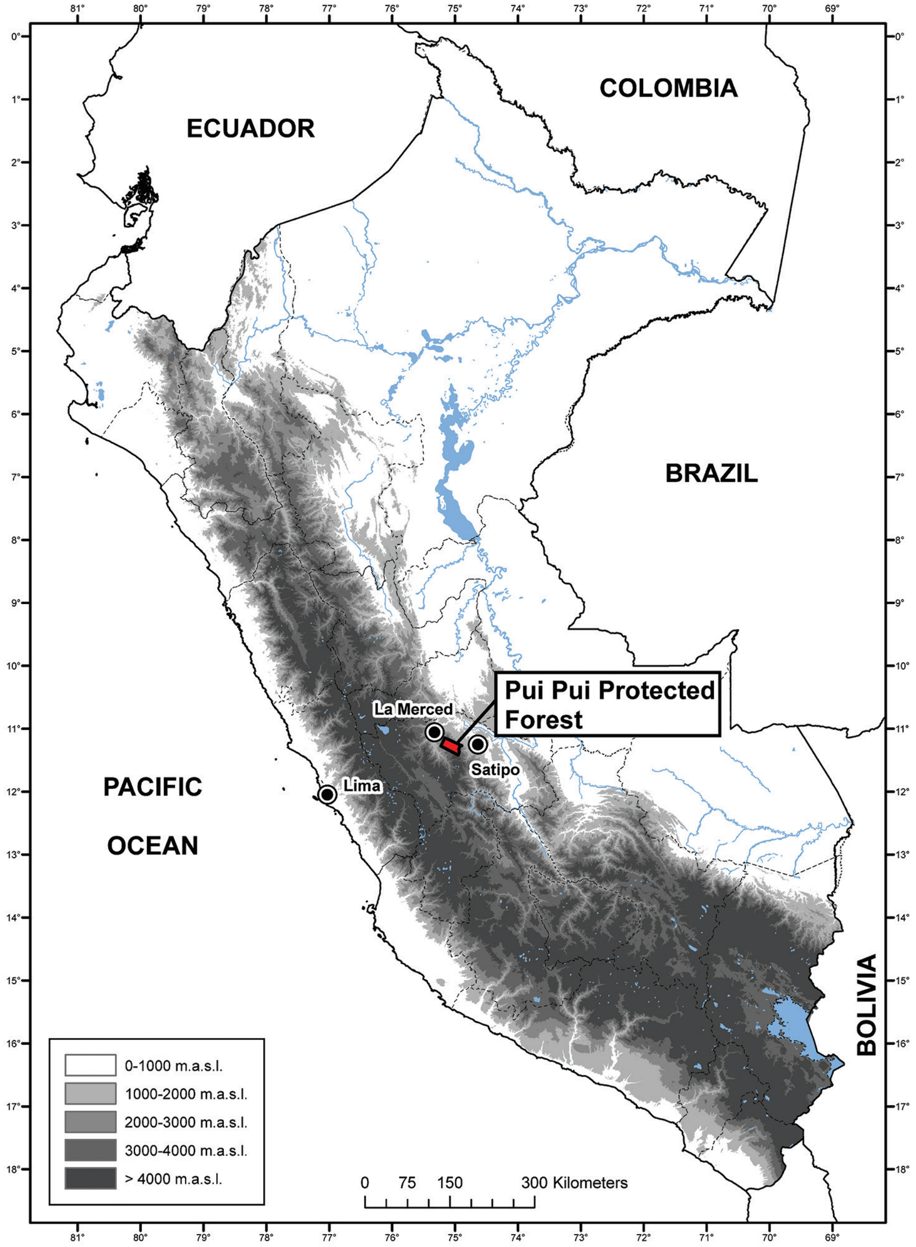

Figure 1. Map of Peru with the Pui Pui Protected Forest indicated in red. Map by J.C. Cusi.

in montane forests and puna habitats between 2600 and 4490 m a.s.l. in northern and central Peru (Rodríguez and Catenazzi 2017, Duellman and Lehr 2009). Herein we name and describe this new species of *Phrynopus*, supported by morphological and phylogenetic evidence, from upper montane forests and puna habitats.

Materials and methods

Fieldwork. The puna of the PPPF was reached by walking 1.5 days along a trail from Toldopama (11°30'15.4"S, 74°55'32.7"W, 3670 m a.s.l., two hours by car from Satipo) to Tarhuish (11°23'23.2"S; 74°57'02.5"W, 3783 m a.s.l.; Fig. 2) with the help of local guides. Fieldwork was conducted in puna and upper montane forests in 2012 between May 8 and 21 by EL and RvM, and in 2013 between June 21 and July 8 by EL, JM, and JCC. Collected specimens were preserved in 96% ethanol and stored in 70% ethanol.

Morphological characters. The format for the description follows Lynch and Duellman (1997), except that the term dentigerous processes of vomers is used instead of vomerine odontophores (Duellman et al. 2006), and diagnostic characters are those of Duellman and Lehr (2009). Taxonomic classification follows Hedges et al. (2008), except that we followed Pyron and Wiens (2011) for family placement. Sex and maturity of specimens were identified by observing gonads through dissections. The senior author measured the following variables to the nearest 0.1 mm with digital calipers under a stereomicroscope: snout-vent length (SVL), tibia length (TL, distance from the knee to the distal end of the tibia), foot length (FL, distance from proximal margin of inner metatarsal tubercle to tip of Toe IV), head length (HL, from angle of jaw to tip of snout), head width (HW, at level of angle of jaw), horizontal eye diameter (ED), interorbital distance (IOD), upper eyelid width (EW), internarial distance (IND), eye-nostril distance (E-N, straight line distance between anterior corner of orbit and posterior margin of external nares), and egg diameter. Fingers and toes are numbered preaxially to postaxially from I–IV and I–V, respectively. We compared the lengths of toes III and V by adpressing both toes against Toe IV; lengths of fingers I and II were compared by adpressing these fingers against each other. All drawings were made using a stereomicroscope and a camera lucida. Photographs of live specimens were used for descriptions of coloration in life and for evaluation of morphological characters that might have been impacted by the preservation process. Information on species for comparative diagnoses was obtained from Duellman and Lehr (2009) and from original species descriptions. For specimens examined see Appendix I. Codes of collections are: **MUSM** – Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **NMP6V** – National Museum, Prague, Czech Republic; **UMMZ** – University of Michigan Museum of Zoology, Ann Arbor, USA. Field number code is: **IWU** – Illinois Wesleyan University, Bloomington, USA. Threat status was evaluated using the IUCN criteria (IUCN Standards an Petitions Subcommittee 2016).

Maps. Maps were made with ArcGIS 10.0 (ESRI 2011). The estimated area was calculated by a minimum convex polygon using known sites of occurrence of the species as defined by IUCN (2012).

Molecular phylogenetic analysis. Our analysis included DNA sequence data from *Phrynopus* species that were available in GenBank (as of 1 August 2017; Table 1) as well as sequences from other closely related genera (*Lynchius*, *Oreobates*) and more distantly related ones (*Ischnocnema guentheri*, *Hypodactylus brunneus*, and *H. dolops*) as outgroups

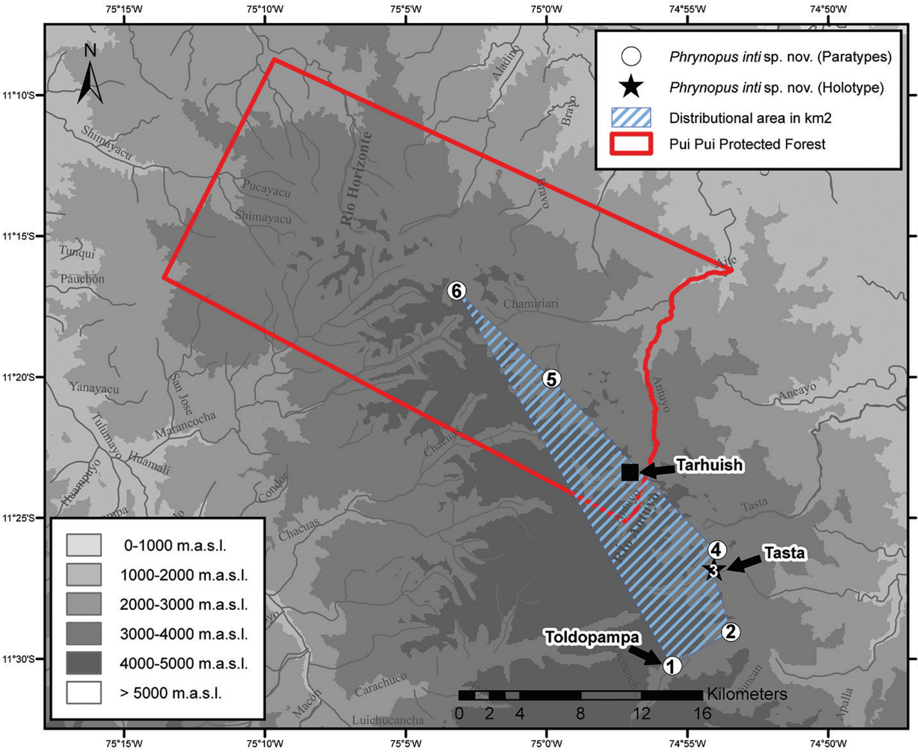

Figure 2. Pui Pui Protected Forest indicated in red outline with collecting sites (1–6) of *Phrynopus inti* **sp. n.**, star indicating type locality, and the estimated distributional area of 101.3 km^2 in blue. 1 = Toldopampa valley, 3670 m a.s.l., 2 = Satipo-Toldopampa Road at km 134, 3350 m a.s.l., 3 = Quebrada Tasta, 3609 m a.s.l., 4 = *Polylepis* forest patch near trail from Tasta to Tarhuish, 3886 m a.s.l., 5 = Antuyo, 3700 m a.s.l., 6 = close to Laguna Sinchon, 3890 m a.s.l. Map by J.C. Cusi.

following the results of Padial et al. (2014). Newly produced sequences include those obtained from seven specimens of the new species and one specimen of *Phrynopus juninensis* collected near Hacienda Cascas, Junín, the type locality of this species (Table 1). Our analysis also included sequences from three mitochondrial and two nuclear genes for several species of *Phrynopus* included in a recent study (De la Riva et al. 2017). The mitochondrial genes were a section of the 16S rRNA gene, a section of the 12S rRNA gene, and the protein-coding gene cytochrome c oxidase subunit I (COI). The nuclear genes were the recombination-activating protein 1 (RAG1) and Tyrosinase precursor (Tyr).

Extraction, amplification, and sequencing of DNA followed protocols previously used for Neotropical terrestrial breeding frogs (Lehr et al. 2005, Hedges et al. 2008). Primers used are listed in Appendix II. We employed the following thermocycling conditions to amplify DNA from each gene using the polymerase chain reaction (PCR). For 16S, we used: 1 cycle of 96 °C/3 min; 35 cycles of 95 °C/30 s, 55 °C/45

Table 1. GenBank accession numbers for the taxa and genes sampled in this study. Bold font indicates new sequences generated for this study. Taxonomy follows Padial et al. (2014).

Taxon	16S	12S	COI	RAG1	Tyr	Voucher_Nbr
Hypodactylus brunneus	EF493357	EF493357	na	EF493422	EF493484	KU178258
Hypodactylus dolops	EF493394	EF493394	na	EF493414	EF493483	na
Ischnocnema guentheri	EF493533	EF493533	na	EF493407	EF493510	na
Lynchius flavomaculatus	EU186667	EU186667	na	EU186745	EU186766	KU218210
Lynchius nebulanastes	EU186704	EU186704	na	na	na	KU181408
Lynchius oblitus	AM039639	AM039707	na	na	na	MTD45954
Lynchius oblitus	AM039640	AM039708	na	na	na	MHSNM19914
Lynchius parkeri	EU186705	EU186705	na	na	na	KU181307
Lynchius simmonsi	JF810004	JF809940	na	JF809915	JF809894	QZ41639
Oreobates amarakaeri	JF809996	JF809934	na	JF809913	JF809891	MHNC6975
Oreobates ayacucho	JF809970	JF809933	na	JF809912	JF809890	MNCN_IDlR5024
Oreobates cruralis	EU186666	EU186666	na	EU186743	EU186764	KU215462
Oreobates gemcare	JF809960	JF809930	na	JF809909	na	MHNC6687
Oreobates granulosus	EU368897	JF809929	na	JF809908	JF809887	MHNC3396
Phrynopus auriculatus	EF493708	EF493708	na	na	na	KU291634
Phrynopus auriculatus	MF186348	MF186290	MF186466	na	MF186582	MUBI 6471
Phrynopus barthlenae	AM039653	AM039721	na	na	na	SMF81720
Phrynopus barthlenae	MF186350	MF186292	MF186464	na	na	MHNSM20609
Phrynopus bracki	EF493709	EF493709	na	EF493421	na	USNM286919
Phrynopus bufoides	AM039645	AM039713	na	na	na	MHNSM19860
Phrynopus heimorum	AM039635	AM039703	MF186462	MF186545	MF186580	MTD45621
Phrynopus heimorum	AM039636	AM039704	na	na	na	MTD45622
Phrynopus horstpauli	AM039647	AM039715	na	na	na	MTD44334
Phrynopus horstpauli	AM039651	AM039719	na	na	na	MTD44333
Phrynopus horstpauli	MF186364	MF186303	na	na	MF186584	MTD44335
Phrynopus inti **sp. n.**	**MF651901**	na	na	**MF651916**	na	MUSM31203
Phrynopus inti **sp. n.**	**MF651902**	**MF651909**	na	**MF651917**	na	MUSM31968
Phrynopus inti **sp. n.**	**MF651903**	**MF651910**	na	na	na	MUSM31976
Phrynopus inti **sp. n.**	**MF651904**	**MF651911**	na	na	na	MUSM31984
Phrynopus inti **sp. n.**	**MF651905**	**MF651912**	na	na	na	NMP6V75584
Phrynopus inti **sp. n.**	**MF651906**	**MF651913**	na	**MF651918**	**MF651921**	UMMZ_245218
Phrynopus inti **sp. n.**	**MF651907**	**MF651914**	na	**MF651919**	na	UMMZ_245219
Phrynopus juninensis	**MF651908**	**MF651915**	na	**MF651920**	na	MUSM33258
Phrynopus kauneorum	AM039650	AM039718	na	na	na	MTD44332
Phrynopus kauneorum	AM039655	AM039723	na	na	na	MHNSM20595
Phrynopus miroslawae	MF186393	MF186312	MF186463	MF186542	MF186585	MUBI 6469
Phrynopus nicoleae	MF186394	MF186313	MF186468	MF186546	MF186577	MUBI 6441
Phrynopus pesantesi	AM039656	AM039724	na	na	na	MTD45072
Phrynopus sp.	AM039657	AM039725	na	na	na	MTD45075
Phrynopus sp.	AM039660	AM039728	na	na	na	MTD44759
Phrynopus tautzorum	AM039652	AM039720	na	na	na	MHNSM20613
Phrynopus tribulosus	EU186725	EU186707	na	na	na	KU291630
Phrynopus tribulosus	MF186423	MF186329	MF186469	na	MF186578	MUBI 6451
Phrynopus tribulosus	MF186424	MF186330	MF186467	MF186547	MF186579	MUBI 7166

s, 72°C/1.5 min; 1 cycle 72°C/7 min. For 12S, we used: 1 cycle of 94°C/1.5 min; 35 cycles of 94°C/45 s, 50°C/1 min., 74°C/2 min; 1 cycle 72°C/10 min. For RAG1, we used: 1 cycle of 96°C/2 min; 40 cycles of 94°C/30 s, 52°C/30 s, 72°C/1.5 min; 1 cycle 72°C/7 min. For Tyr, we used: 1 cycle of 94°C/5 min; 40 cycles of 94°C/30 s, 54°C/30 s, 72°C/1 min; 1 cycle 72°C/7 min. We completed the cycle sequencing reactions by using the corresponding PCR primers and the BigDye Terminator 3.1 (Applied Biosystems), and obtained sequence data by running the purified reaction products in an ABI 3730 Sequence Analyzer (Applied Biosystems). We deposited the newly obtained sequences in GenBank (Table 1).

We used Geneious R6, version 6.1.8 (Biomatters 2013; http://www.geneious.com/) to align the sequences with the built-in multiple alignment program. Prior to conducting phylogenetic analysis, we used PartitionFinder, version 1.1.1 (Lanfear et al. 2012) to select the appropriate models of nucleotide evolution and used the Bayesian information criterion (BIC) to determine the best partitioning scheme and substitution model for each gene. The best partitioning scheme included five subsets (BIC value: 27719.16). The first partition subset included both the 12S and 16S sequences and the best fitting substitution model was GTR+I+G. The remaining four subsets were partitioned according to codon positions as follows (substitution model in parenthesis): one set including the 1st codon position of COI and the 3rd codon position of both RAG1 and Tyr (K80+G); one set with only the 2nd codon position of COI (HKY); one set with only the 3rd codon position of COI (HKY); one set including the 1st and 2nd codon position of RAG1 and the 1st and 2nd codon position of Tyr (HKY+I).

We employed a Bayesian approach using MrBayes, version 3.2.0 (Ronquist and Huelsenbeck 2003) to infer a molecular phylogeny. Our analysis included 44 terminals and a 2684-bp concatenated partitioned dataset. We performed an MCMC Bayesian analysis that consisted of two simultaneous runs of 8 million generations, and we set the sampling rate to be once every 1000 generations. Each run had three heated chains and one "cold" chain, and the burn-in was set to discard the first 25% samples from the cold chain. At the end of the run, the average standard deviation of split frequencies was 0.002257. Following the completion of the analysis, we used Tracer 1.6 (Rambaut and Drummond 2003) to verify convergence. Subsequently, we used FigTree (http://tree.bio.ed.ac.uk/software/figtree/) to visualize the majority-rule consensus tree and the posterior probability values to assess node support. Additionally, we used the R package 'APE' (Paradis et al. 2004) to estimate uncorrected p-distances (i.e., the proportion of nucleotide sites at which any two sequences are different).

Results

Molecular phylogenetic analysis. Placement of the new species in the genus *Phrynopus* was strongly supported by this analysis. We recovered a well-supported tree (Figure 3) that was generally congruent with previous trees (Padial et al. 2014) and sup-

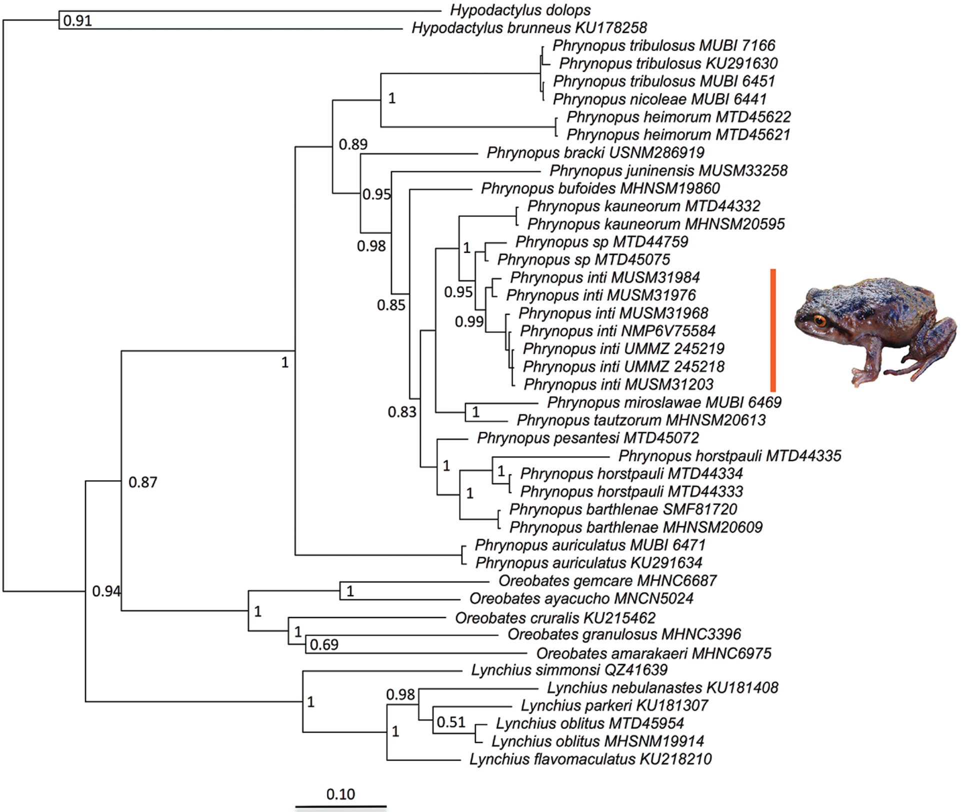

Figure 3. Bayesian maximum clade-credibility tree for species included in this study based on a 2684-bp concatenated partitioned dataset (16S, 12S, COI, RAG1, Tyr) analyzed in MrBayes (posterior probabilities are indicated at each node).

ported the unique history of divergence of the new species from other closely related taxa including *Phrynopus kauneorum* Lehr, Aguilar, & Köhler, 2002a, *P. miroslawae* Chaparro, Padial, & De la Riva, 2008, *P. tautzorum* Lehr & Aguilar, 2002, and an undescribed species. Based on the available data, the new species is most closely related to an undescribed species of *Phrynopus* distributed at high elevation (3600–3850 m a.s.l., Lehr et al. 2005) in Región Pasco. This newly identified cryptic species was previously recognized as *P. juninensis* Shreve, 1938 given their similar morphology and coloration (Lehr et al. 2005, Padial et al. 2014) and will be formally named and described in a future paper. The uncorrected p-distances between the new species and all other species of *Phrynopus* ranged between 4.5 and 14.1% (Table 2). The shortest distance occurs between the new species and the undescribed species (uncorrected p-distance 1.5–2.8%) while the uncorrected p-distances between *P. kauneorum* and the new species vary between 3.7 to 4.8% (Table 2). Our analysis also suggests that *P. nicoleae* Chaparro, Padial, & De la Riva, 2008 and *P. tribulosus* Duellman & Hedges, 2008 might represent one species.

Table 2. Uncorrected p-distances of the 16S mitochondrial rRNA gene for 30 specimens of *Phrynopus*, including the new species.

		1	**2**	**3**	**4**	**5**	**6**	**7**
1	*Phrynopus auriculatus* KU291634	0.000						
2	*Phrynopus auriculatus* MUBI 6471	0.002	0.000					
3	*Phrynopus barthlenae* MHNSM20609	0.138	0.135	0.000				
4	*Phrynopus barthlenae* SMF81720	0.118	0.115	0.000	0.000			
5	*Phrynopus horstpauli* MTD44333	0.114	0.112	0.040	0.039	0.000		
6	*Phrynopus horstpauli* MTD44334	0.114	0.112	0.040	0.039	0.000	0.000	
7	*Phrynopus horstpauli* MTD44335	0.115	0.112	0.040	0.039	0.000	0.000	0.000
8	*Phrynopus pesantesi* MTD45072	0.105	0.103	0.040	0.037	0.035	0.035	0.035
9	*Phrynopus bufoides* MHNSM19860	0.121	0.119	0.073	0.064	0.060	0.060	0.060
10	*Phrynopus tautzorum* MHNSM20613	0.119	0.116	0.077	0.070	0.066	0.066	0.066
11	*Phrynopus miroslawae* MUBI 6469	0.132	0.130	0.084	0.072	0.074	0.074	0.074
12	***Phrynopus inti* MUSM31203**	0.125	0.123	0.080	0.070	0.072	0.072	0.073
13	***Phrynopus inti* UMMZ 245218**	0.125	0.123	0.080	0.070	0.072	0.072	0.073
14	***Phrynopus inti* UMMZ 245219**	0.125	0.123	0.080	0.070	0.072	0.072	0.073
15	***Phrynopus inti* MUSM31968**	0.125	0.123	0.080	0.070	0.072	0.072	0.073
16	***Phrynopus inti* NMP6V75584**	0.128	0.126	0.082	0.072	0.075	0.075	0.075
17	***Phrynopus inti* MUSM31976**	0.123	0.121	0.070	0.064	0.068	0.068	0.069
18	***Phrynopus inti* MUSM31984**	0.131	0.128	0.070	0.064	0.066	0.066	0.067
19	*Phrynopus* sp. MTD45075	0.114	0.112	0.069	0.062	0.056	0.056	0.056
20	*Phrynopus* sp. MTD44759	0.119	0.117	0.064	0.059	0.053	0.053	0.053
21	*Phrynopus kauneorum* MHNSM20595	0.128	0.125	0.088	0.079	0.081	0.081	0.082
22	*Phrynopus kauneorum* MTD44332	0.128	0.125	0.088	0.079	0.081	0.081	0.082
23	*Phrynopus bracki* USNM286919	0.110	0.108	0.082	0.074	0.074	0.074	0.075
24	*Phrynopus juninensis* MUSM33258	0.141	0.138	0.126	0.109	0.114	0.114	0.115
25	*Phrynopus heimorum* MTD45621	0.146	0.143	0.137	0.124	0.124	0.124	0.125
26	*Phrynopus heimorum* MTD45622	0.146	0.143	0.137	0.124	0.124	0.124	0.125
27	*Phrynopus nicoleae* MUBI 6441	0.137	0.135	0.124	0.108	0.111	0.111	0.112
28	*Phrynopus tribulosus* KU291630	0.137	0.134	0.124	0.108	0.111	0.111	0.112
29	*Phrynopus tribulosus* MUBI 6451	0.136	0.134	0.124	0.110	0.110	0.110	0.111
30	*Phrynopus tribulosus* MUBI 7166	0.136	0.134	0.124	0.110	0.110	0.110	0.111

		8	**9**	**10**	**11**	**12**	**13**	**14**
1	*Phrynopus auriculatus* KU291634							
2	*Phrynopus auriculatus* MUBI 6471							
3	*Phrynopus barthlenae* MHNSM20609							
4	*Phrynopus barthlenae* SMF81720							
5	*Phrynopus horstpauli* MTD44333							
6	*Phrynopus horstpauli* MTD44334							
7	*Phrynopus horstpauli* MTD44335							
8	*Phrynopus pesantesi* MTD45072	0.000						
9	*Phrynopus bufoides* MHNSM19860	0.051	0.000					
10	*Phrynopus tautzorum* MHNSM20613	0.058	0.064	0.000				
11	*Phrynopus miroslawae* MUBI 6469	0.068	0.082	0.049	0.000			
12	***Phrynopus inti* MUSM31203**	0.054	0.063	0.066	0.068	0.000		
13	***Phrynopus inti* UMMZ 245218**	0.054	0.063	0.066	0.068	0.000	0.000	
14	***Phrynopus inti* UMMZ 245219**	0.054	0.063	0.066	0.068	0.000	0.000	0.000

15	***Phrynopus inti* MUSM31968**	0.054	0.063	0.066	0.068	0.000	0.000	0.000
16	***Phrynopus inti* NMP6V75584**	0.054	0.063	0.070	0.072	0.000	0.000	0.000
17	***Phrynopus inti* MUSM31976**	0.048	0.054	0.062	0.064	0.017	0.017	0.017
18	***Phrynopus inti* MUSM31984**	0.049	0.054	0.067	0.073	0.023	0.023	0.023
19	*Phrynopus* sp. MTD45075	0.039	0.051	0.049	0.062	0.023	0.023	0.023
20	*Phrynopus* sp. MTD44759	0.042	0.055	0.053	0.065	0.028	0.028	0.028
21	*Phrynopus kauneorum* MHNSM20595	0.052	0.070	0.069	0.077	0.045	0.045	0.045
22	*Phrynopus kauneorum* MTD44332	0.052	0.070	0.069	0.077	0.045	0.045	0.045
23	*Phrynopus bracki* USNM286919	0.068	0.069	0.081	0.075	0.081	0.081	0.081
24	*Phrynopus juninensis* MUSM33258	0.109	0.114	0.117	0.114	0.118	0.118	0.118
25	*Phrynopus heimorum* MTD45621	0.134	0.147	0.136	0.142	0.133	0.133	0.133
26	*Phrynopus heimorum* MTD45622	0.134	0.147	0.136	0.142	0.133	0.133	0.133
27	*Phrynopus nicoleae* MUBI 6441	0.114	0.120	0.136	0.143	0.128	0.128	0.128
28	*Phrynopus tribulosus* KU291630	0.114	0.120	0.136	0.143	0.128	0.128	0.128
29	*Phrynopus tribulosus* MUBI 6451	0.113	0.120	0.136	0.140	0.129	0.129	0.129
30	*Phrynopus tribulosus* MUBI 7166	0.113	0.120	0.136	0.140	0.129	0.129	0.129
		15	**16**	**17**	**18**	**19**	**20**	**21**
1	*Phrynopus auriculatus* KU291634							
2	*Phrynopus auriculatus* MUBI 6471							
3	*Phrynopus barthlenae* MHNSM20609							
4	*Phrynopus barthlenae* SMF81720							
5	*Phrynopus horstpauli* MTD44333							
6	*Phrynopus horstpauli* MTD44334							
7	*Phrynopus horstpauli* MTD44335							
8	*Phrynopus pesantesi* MTD45072							
9	*Phrynopus bufoides* MHNSM19860							
10	*Phrynopus tautzorum* MHNSM20613							
11	*Phrynopus miroslawae* MUBI 6469							
12	***Phrynopus inti* MUSM31203**							
13	***Phrynopus inti* UMMZ 245218**							
14	***Phrynopus inti* UMMZ 245219**							
15	***Phrynopus inti* MUSM31968**	0.000						
16	***Phrynopus inti* NMP6V75584**	0.000	0.000					
17	***Phrynopus inti* MUSM31976**	0.017	0.018	0.000				
18	***Phrynopus inti* MUSM31984**	0.023	0.023	0.008	0.000			
19	*Phrynopus* sp. MTD45075	0.023	0.024	0.015	0.016	0.000		
20	*Phrynopus* sp. MTD44759	0.028	0.029	0.022	0.017	0.008	0.000	
21	*Phrynopus kauneorum* MHNSM20595	0.045	0.048	0.037	0.040	0.043	0.049	0.000
22	*Phrynopus kauneorum* MTD44332	0.045	0.048	0.037	0.040	0.043	0.049	0.000
23	*Phrynopus bracki* USNM286919	0.081	0.084	0.079	0.083	0.073	0.077	0.086
24	*Phrynopus juninensis* MUSM33258	0.118	0.119	0.113	0.116	0.115	0.116	0.113
25	*Phrynopus heimorum* MTD45621	0.133	0.137	0.141	0.141	0.133	0.135	0.146
26	*Phrynopus heimorum* MTD45622	0.133	0.137	0.141	0.141	0.133	0.135	0.146
27	*Phrynopus nicoleae* MUBI 6441	0.128	0.128	0.130	0.125	0.123	0.119	0.133
28	*Phrynopus tribulosus* KU291630	0.128	0.128	0.130	0.125	0.123	0.119	0.133
29	*Phrynopus tribulosus* MUBI 6451	0.129	0.129	0.132	0.126	0.124	0.120	0.135
30	*Phrynopus tribulosus* MUBI 7166	0.129	0.129	0.132	0.126	0.124	0.120	0.135

		22	**23**	**24**	**25**	**26**	**27**	**28**
1	*Phrynopus auriculatus* KU291634							
2	*Phrynopus auriculatus* MUBI 6471							
3	*Phrynopus barthlenae* MHNSM20609							
4	*Phrynopus barthlenae* SMF81720							
5	*Phrynopus horstpauli* MTD44333							
6	*Phrynopus horstpauli* MTD44334							
7	*Phrynopus horstpauli* MTD44335							
8	*Phrynopus pesantesi* MTD45072							
9	*Phrynopus bufoides* MHNSM19860							
10	*Phrynopus tautzorum* MHNSM20613							
11	*Phrynopus miroslawae* MUBI 6469							
12	***Phrynopus inti* MUSM31203**							
13	***Phrynopus inti* UMMZ 245218**							
14	***Phrynopus inti* UMMZ 245219**							
15	***Phrynopus inti* MUSM31968**							
16	***Phrynopus inti* NMP6V75584**							
17	***Phrynopus inti* MUSM31976**							
18	***Phrynopus inti* MUSM31984**							
19	*Phrynopus* sp. MTD45075							
20	*Phrynopus* sp. MTD44759							
21	*Phrynopus kauneorum* MHNSM20595							
22	*Phrynopus kauneorum* MTD44332	0.000						
23	*Phrynopus bracki* USNM286919	0.086	0.000					
24	*Phrynopus juninensis* MUSM33258	0.113	0.105	0.000				
25	*Phrynopus heimorum* MTD45621	0.146	0.118	0.113	0.000			
26	*Phrynopus heimorum* MTD45622	0.146	0.118	0.113	0.000	0.000		
27	*Phrynopus nicoleae* MUBI 6441	0.133	0.111	0.121	0.119	0.119	0.000	
28	*Phrynopus tribulosus* KU291630	0.133	0.111	0.121	0.119	0.119	0.000	0.000
29	*Phrynopus tribulosus* MUBI 6451	0.135	0.110	0.123	0.121	0.121	0.002	0.002
30	*Phrynopus tribulosus* MUBI 7166	0.135	0.110	0.123	0.121	0.121	0.002	0.002

		29	**30**					
1	*Phrynopus auriculatus* KU291634							
2	*Phrynopus auriculatus* MUBI 6471							
3	*Phrynopus barthlenae* MHNSM20609							
4	*Phrynopus barthlenae* SMF81720							
5	*Phrynopus horstpauli* MTD44333							
6	*Phrynopus horstpauli* MTD44334							
7	*Phrynopus horstpauli* MTD44335							
8	*Phrynopus pesantesi* MTD45072							
9	*Phrynopus bufoides* MHNSM19860							
10	*Phrynopus tautzorum* MHNSM20613							
11	*Phrynopus miroslawae* MUBI 6469							
12	***Phrynopus inti* MUSM31203**							
13	***Phrynopus inti* UMMZ 245218**							
14	***Phrynopus inti* UMMZ 245219**							
15	***Phrynopus inti* MUSM31968**							

16	***Phrynopus inti* NMP6V75584**							
17	***Phrynopus inti* MUSM31976**							
18	***Phrynopus inti* MUSM31984**							
19	*Phrynopus* sp. MTD45075							
20	*Phrynopus* sp. MTD44759							
21	*Phrynopus kauneorum* MHNSM20595							
22	*Phrynopus kauneorum* MTD44332							
23	*Phrynopus bracki* USNM286919							
24	*Phrynopus juninensis* MUSM33258							
25	*Phrynopus heimorum* MTD45621							
26	*Phrynopus heimorum* MTD45622							
27	*Phrynopus nicoleae* MUBI 6441							
28	*Phrynopus tribulosus* KU291630							
29	*Phrynopus tribulosus* MUBI 6451	0.000						
30	*Phrynopus tribulosus* MUBI 7166	0.000	0.000					

***Phrynopus inti* sp. n.**

http://zoobank.org/C3E88CD6-7AD2-4CFE-8129-A6DB6D747F70

Phrynopus sp. A in Lehr, von May, Moravec, & Cusi (2017)

Common name. English: Inti Andes Frog. Spanish: Rana Andina Inti.

Holotype (Figs 4A,B, 5, 6). MUSM 31183 (IWU 155), adult male from the buffer zone of the Pui Pui Protected Forest, Quebrada Tasta, forest patch near the house of Evaristo Bórquez Quintana, 11°26'48.8"S, 74°54’2.8"W, 3609 m a.s.l. (Figs 2, 10C), Provincia Satipo, Región Junín, Peru, collected on 9 May 2012 by E. Lehr and R. von May.

Paratypes (Figs 7, 8, 9). A total of 15, all from Provincia Satipo, Región Junín, Peru (for detailed information see below): 5 males (MUSM 31976, 31984, 31203, NMP6V 75584, UMMZ 245220), 1 female (MUSM 31968), 9 juveniles (MUSM 31184, 31969, 31974, 31985, NMP6V 75585–87, UMMZ 245218, 245219).

MUSM 31184, UMMZ 245218, 245219, collected with the holotype on 9 May 2012 by E. Lehr and R. von May; MUSM 31203, near trail from Tasta to Tarhuish (first cumbre), *Polylepis* forest patch, 11°26'8.6"S, 74°53'56.5"W, 3886 m a.s.l. collected on 20 May 2012 by E. Lehr and R. von May; MUSM 31968, 31969, UMMZ 245220, Toldopampa, 11°30'15"S, 74°55'33"W, 3670 m a.s.l., collected on 22 June 2013 by E. Lehr, J. Moravec, and J.C. Cusi; NMP6V 75584, from Sector Carrizal, Satipo-Toldopampa Road at km 134 on left side of road coming from Satipo, 11°29'03.5"S, 74°53'27.3"W, 3350 m a.s.l., collected on 23 June 2013 by E. Lehr, J.C. Cusi, and J. Moravec; MUSM 31974, 31976, NMP6V 75585, Antuyo, 11°20'03.7"S, 74°59'49.1"W, 3700 m a.s.l., collected on 27 June 2013 by E. Lehr, J.C. Cusi, and J. Moravec; MUSM 31984, 31985, NMP6V 75586, 75587, Laguna Sinchon, 11°16'56.3"S, 75°03'11.7"W, 3890 m, collected on 30 June 2013 by E. Lehr, J.C. Cusi, and J. Moravec.

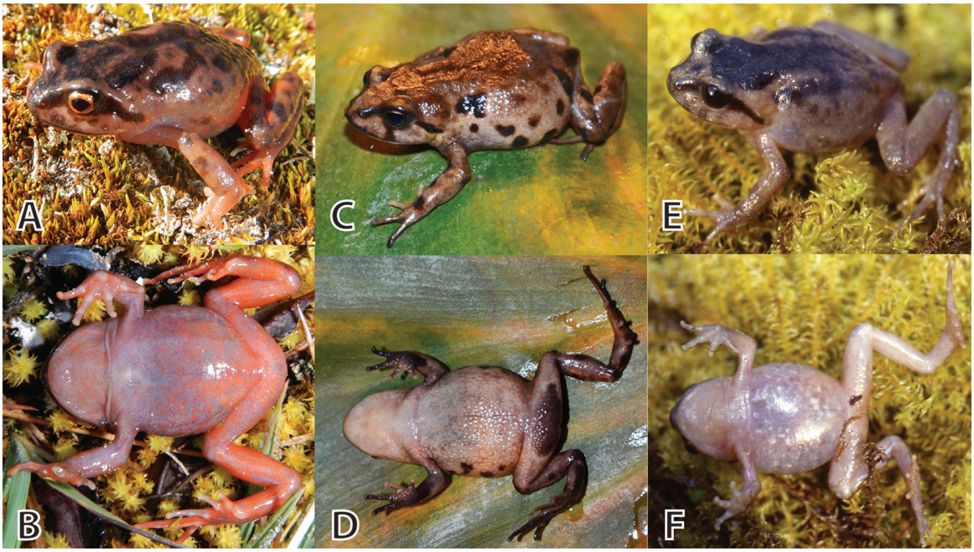

Figure 4. *Phrynopus inti* sp. n. (**A, B** holotype, MUSM 31183, male, SVL 32.5 mm), *P. juninensis* (**C, D** MUSM 33258, female, SVL 33.0 mm), *P. kauneorum* (**E, F** holotype, MUSM 20459, female, SVL 29.1 mm) in dorsolateral and ventral views. Photos by E. Lehr and R. von May (**C, D**).

Generic placement. We assign this species to *Phrynopus* based on molecular evidence (Fig. 3).

Diagnosis. A species of *Phrynopus* having the following combination of characters: (1) Skin on dorsum and flanks shagreen with scattered, low tubercles, more dense on dorsum; skin on venter smooth; discoidal fold absent, thoracic fold present; prominent supratympanic fold; dorsolateral folds absent; (2) tympanic membrane and tympanic annulus absent; (3) snout rounded in dorsal and lateral views; (4) upper eyelid without enlarged tubercles; width of upper eyelid narrower than IOD; cranial crests absent; (5) dentigerous processes of vomers minute or absent; (6) vocal slits and nuptial pads absent; (7) Finger I shorter than Finger II; tips of digits bulbous, rounded; (8) fingers without lateral fringes; (9) ulnar and tarsal tubercles absent; (10) heel without tubercles; inner tarsal fold absent; (11) inner metatarsal tubercle rounded, about three times as large as ovoid outer metatarsal tubercle; supernumerary plantar tubercles absent; (12) toes without lateral fringes; basal webbing absent; Toe V slightly longer than Toe III; toe tips bulbous, rounded, about as large as those on fingers; (13) in life, dorsum pale grayish brown with or without dark brown blotches or blackish brown with small yellow flecks; throat, chest and venter pale grayish brown with salmon mottling, groin pale grayish brown with salmon colored flecks; iris golden orange with fine dark brown reticulations; (14) SVL 27.2–35.2 mm in males (n = 6), and 40.4 mm in single female.

Comparisons. *Phrynopus inti* sp. n. is readily distinguished from its 34 congeners in Peru (AmphibiaWeb 2017), by its relatively large SVL (except for *P. juninensis* and *P. kauneorum*) of up to 40.4 mm, by having the groin pale grayish brown with salmon colored flecks, the venter pale grayish brown with salmon mottling and the iris golden orange with fine dark brown reticulations. *Phrynopus inti* sp. n. is most similar to the large central Peruvian species *P. juninensis* (SVL up to 43.1 mm, Duellman and Lehr 2009) and *P. kauneorum* (SVL up to 56.4 mm, Lehr et al. 2002b), Fig. 4. All three species share a gray ground coloration and dark brown canthal and supratympanic stripes, lack dorsolateral folds and males lack vocal slits and nuptial pads, but can be distinguished as follows: *Phrynopus inti* sp. n. has weak postocular folds (absent in both *P. juninensis* and *P. kauneorum*), has dentigerous processes of vomers (absent in *P. juninensis,* present in *P. kauneorum*), skin on dorsum shagreen with scattered, low tubercles (smooth to weakly areolate in *P. juninensis,* smooth in *P. kauneorum*), skin on venter smooth (areolate in *P. juninensis,* smooth in *P. kauneorum*), dorsum pale grayish brown with or without dark brown blotches or blackish brown with small yellow flecks (dorsum grayish brown with dark brown markings in *P. juninensis,* dorsum pale brown to tan with dark brown markings in *P. kauneorum*), venter pale grayish brown with salmon mottling (pale brown with gray blotches in *P. juninensis,* pinkish to grayish tan in *P. kauneorum*), and the iris is golden orange (copper in *P. juninensis,* dark brown in *P. kauneorum*).

Description of the holotype. Head as wide as body, wider than long, HW 110% of HL; HW 38% of SVL; HL 35% of SVL; snout short, rounded in dorsal and lateral views (Figs 5A, B), ED larger than E–N distance (ED 148% of E–N); nostrils protuberant, directed dorsolaterally; canthus rostralis slightly curved in dorsal view, rounded in profile; loreal region slightly concave; lips rounded; upper eyelid without enlarged tubercles; EW slightly narrower than IOD (EW 94% of IOD); postocular folds low, extending from posterior margin of upper eyelid to level of upper arm insertion (Fig. 5B); supratympanic fold broad, extending from posterior corner of eye to level of upper arm insertion; tympanic membrane and tympanic annulus absent, tympanic region without postrictal tubercles. Choanae small, ovoid, close to but not concealed by palatal shelf of maxilla; dentigerous processes of vomers minute, embedded in mucosa of mouth, widely separated; tongue broad, about twice as long as wide, not notched posteriorly, posterior half free; vocal slits absent.

Skin on dorsum shagreen with scattered, low tubercles, more dense on posterior half of body, dorsolateral folds absent (Fig. 5B); skin on flanks shagreen with few scattered, low tubercles; skin on throat, chest and belly smooth (Fig. 5D); discoidal fold absent, thoracic fold present; cloacal sheath not distinct; cloacal region without tubercles. Outer surface of forearm without tubercles; outer palmar tubercle barely visible, low, ovoid, slightly smaller than ovoid inner palmar tubercle; supernumerary tubercles absent; subarticular tubercles low, ovoid, most prominent on base of fingers; fingers without lateral fringes; Finger I shorter than Finger II; tips of digits rounded, bulbous, lacking circumferential grooves; nuptial pads absent (Fig. 6A).

Hind limbs long and slender, TL 39% of SVL; FL 43% of SVL; dorsal surface of hind limbs shagreen with few low tubercles; anterior surfaces of thighs shagreen, posterior surfaces of thighs weakly areolate; heel without a conical tubercle; outer surface of tarsus without tubercles; outer metatarsal tubercle rounded, weakly conical, about four times as large as prominent ovoid inner metatarsal tubercle; supernumerary plantar

Figure 5. Life male holotype (MUSM 31183, SVL 32.5 mm) of *Phrynopus inti* sp. n. in dorsolateral view (**A**), dorsal view (**B**), flanks, groin, anterior surfaces of thighs (**C**), and ventral view (**D**). Photos by E. Lehr.

tubercles absent; subarticular tubercles low, ovoid in dorsal view, most distinct on base of toes; toes without lateral fringes; basal webbing absent; toe tips bulbous, rounded, lacking circumferential grooves, about as large as those on fingers; relative lengths of toes: 1 < 2 < 3 < 5 < 4; Toe V slightly longer than Toe III (Fig. 6B).

Measurements of the holotype (in mm). SVL 32.5; tibia length 12.7; foot length 14.0; head length 11.3; head width 12.5; eye diameter 3.4; interorbital distance 3.5; upper eyelid width 3.3; internarial distance 2.9; eye-nostril distance 2.3.

Coloration of the holotype in life (Fig. 5). Dorsum pale grayish brown with dark brown blotches, a dark brown X-shaped marking on shoulder region and an irregular shaped dark brown interorbital blotch. Flanks paler than dorsum with few pale brown flecks. Canthal and supratympanic stripes dark brown. Upper lip with few pale brown flecks. Arms and legs dorsally with few pale and dark brown blotches and flecks. Throat, chest and venter pale grayish brown with salmon mottling, denser on posterior half of belly and thighs. Groin, posterior surfaces of thighs, posterior surfaces of tibias and dorsal surfaces of feet vibrant salmon colored. Iris golden orange with fine dark brown reticulations.

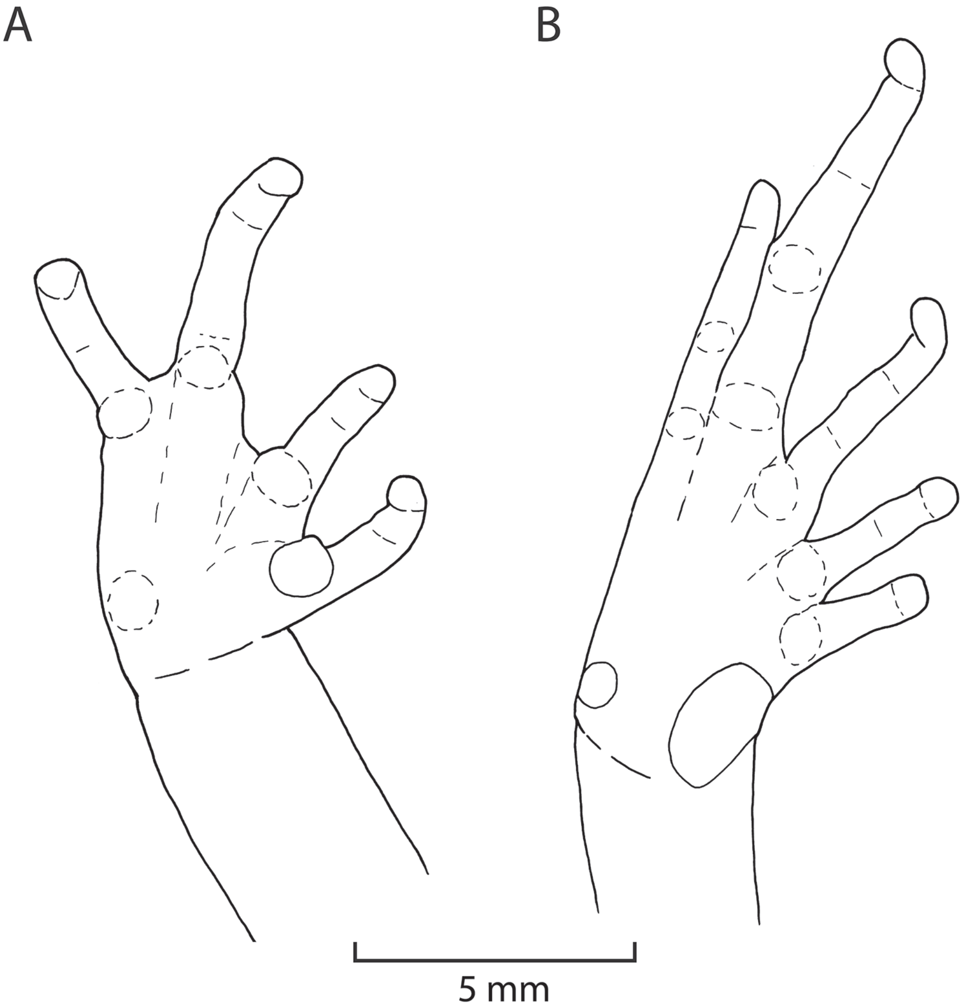

Figure 6. Ventral views of right hand (**A**) and right foot (**B**) of holotype of *Phrynopus inti* sp. n. (MUSM 31183). Drawings by E. Lehr.

Coloration of the holotype in preservative. Dorsum tan with dark brown blotches and dark brown X-shaped marking on shoulder region and an irregular shaped dark brown interorbital blotch. Flanks paler than dorsum, with few pale brown flecks. Canthal and supratympanic stripes dark brown. Upper lip with few pale brown flecks. Arms and legs dorsally tan with few pale and dark brown blotches and flecks. Groin creamy white. Throat, chest and venter creamy white and pale gray mottled. Ventral surfaces of hand and feet creamy white. Iris pale gray.

Variation. All paratypes (Figs 7–9) are similar to the holotype regarding morphology and proportions (Tables 3, 4). Besides differences in SVL (Tables 3, 4), coloration variation in life is notable. Three males (MUSM 31203, UMMZ 245220 (Fig. 7A–C),

Table 3. Measurements (in mm) of adult type specimens of *Phrynopus inti* sp. n. M = male, F = female. For other abbreviations see materials and methods.

Characters	**MUSM 31203**	**UMMZ 245220**	**MUSM 31183**	**NMP6V 75584**	**MUSM 31984**	**MUSM 31976**	**MUSM 31968**
Sex	M	M	M	M	M	M	F
SVL	27.2	27.4	32.5	34.2	35.1	35.2	40.4
TL	10.3	9.9	12.7	14.0	13.3	14.0	15.7
FL	12.2	11.6	14.0	15.4	13.7	13.8	17.1
HL	9.4	9.9	11.3	11.4	11.9	13.0	13.5
HW	10.5	10.6	12.5	12.2	12.6	13.4	14.5
ED	2.4	2.7	3.4	3.1	3.4	3.1	3.5
IOD	3.0	2.8	3.5	3.7	3.0	3.7	3.5
EW	2.5	2.4	3.3	3.2	2.8	3.3	3.4
IND	2.1	2.5	2.9	2.7	2.6	2.9	3.1
E–N	1.9	1.9	2.3	2.1	2.5	2.6	3.0

Table 4. Measurements (in mm) and proportions of male type specimens of *Phrynopus inti* sp. n.; ranges followed by means and one standard deviation in parentheses. For abbreviations see materials and methods.

Characters	*Phrynopus inti* sp. n.
	Males (n = 6)
SVL	27.2–35.2 (31.9 ± 3.4)
TL	9.9–14.4 (12.4 ± 1.7)
FL	11.6–15.4 (13.5 ± 1.2)
HL	9.4–13.0 (11.2 ± 1.2)
HW	10.5–13.4 (12.0 ± 1.1)
ED	2.4–3.4 (3.0 ± 0.4)
IOD	2.8–3.7 (3.3 ± 0.4)
EW	2.4–3.3 (2.9 ± 0.4)
IND	2.1–2.9 (2.6 ± 0.3)
E–N	1.9–2.6 (2.2 ± 0.3)
TL/SVL	0.36–0.41
FL/SVL	0.39–0.45
HL/SVL	0.33–0.37
HW/SVL	0.36–0.39
HW/HL	1.00–1.10
E–N/ED	0.68–0.84
EW/IOD	0.83–0.94

285) are similar to the holotype in coloration except for having much less salmon coloration. One male (MUSM 31976, Fig. 7D–F) has the dorsum uniformly grayish brown without dark brown blotches. One male (MUSM 31984, Fig. 7G–I) has the dorsum blackish brown with small yellow flecks. The single female (MSUM 31968, Fig. 8) is similar in coloration to the holotype except for only having few small flecks of salmon

Figure 7. Variation of male paratypes of *Phrynopus inti* **sp. n.** in dorsolateral, dorsal, and ventral views. **A–C** (UMMZ 245220, SVL 27.4 mm), **D–F** (MUSM 31976, SVL 35.2 mm), **G–I** (MSUM 31984, SVL 35.1 mm). Photos by E. Lehr, and by J.C. Cusi (**E**).

in groin, and ventrally on thighs and shanks. The dorsal coloration of the juveniles (Fig. 9) is similar to the adults (dorsum pale grayish brown with dark brown blotches in MUSM 31969 [Fig. 9A, B], 31974, NMP6V 75585, blackish brown with small yellow flecks in NMP6V 75586, 75587 [Fig. 9D, E], uniformly blackish brown in MUSM 31985). The ventral coloration is different in juveniles. One juvenile (MSUM 31969, Fig. 9C) has the venter reddish brown, three juveniles (MUSM 31974, NMP6V 75585, 75587 (Fig. 9F)) have the venter reddish brown and tan mottled.

Etymology. The species epithet *inti* is derived from the Quechuan noun "Inti", the Incan sun god. The golden-orange iris reminds us of the sun.

Distribution, natural history, and threat status. *Phrynopus inti* sp. n. is known from four localities outside and two localities inside the Pui Pui Protected Forest between 3350 and 3890 m a.s.l., covering an estimated area of 101.3 km^2 (Figs 1, 2).

The type locality, Quebrada Tasta (Fig. 2), is outside the PPPF. The holotype and three paratypes (MUSM 31184, UMMZ 245218, 245219) were found in the afternoon in a forest patch under rocks near the house of Evaristo Bórquez Quintana, on 9 May

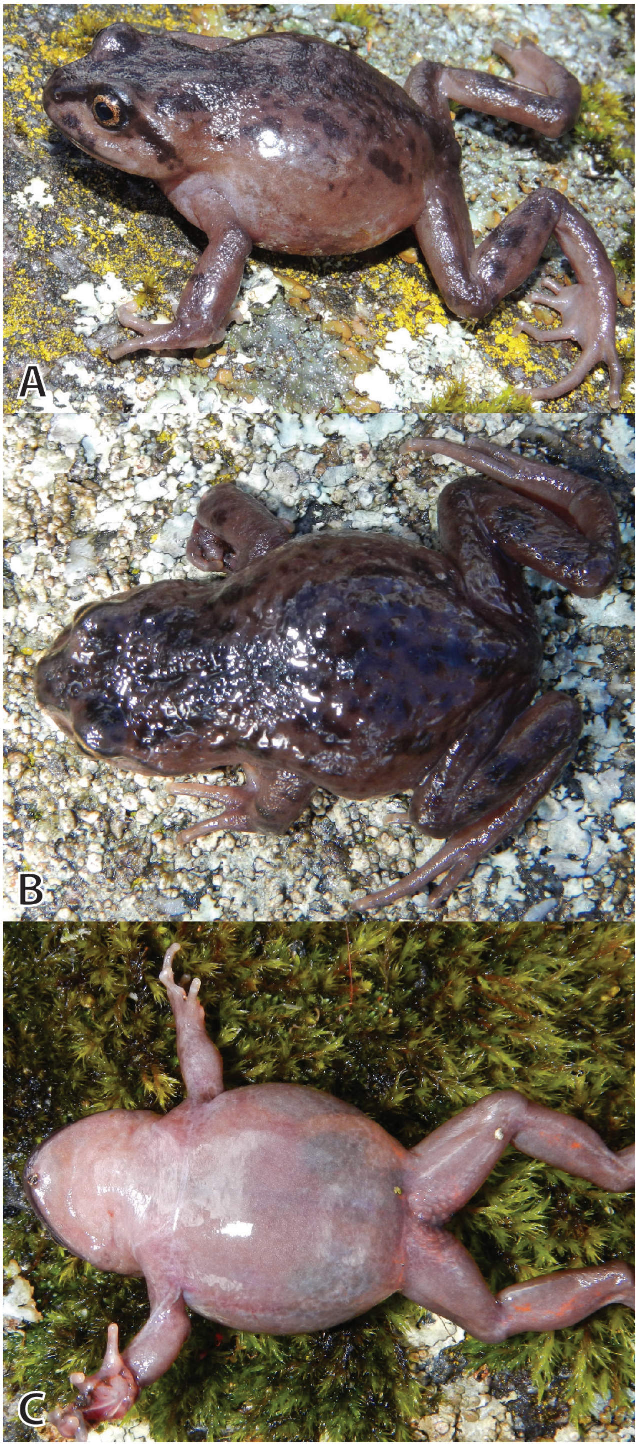

Figure 8. Female paratype of *Phrynopus inti* **sp. n.** (MUSM 31968, SVL 40.4 mm) in dorsolateral (**A**), dorsal (**B**), and ventral views (**C**). Photos by E. Lehr and J. Moravec (A).

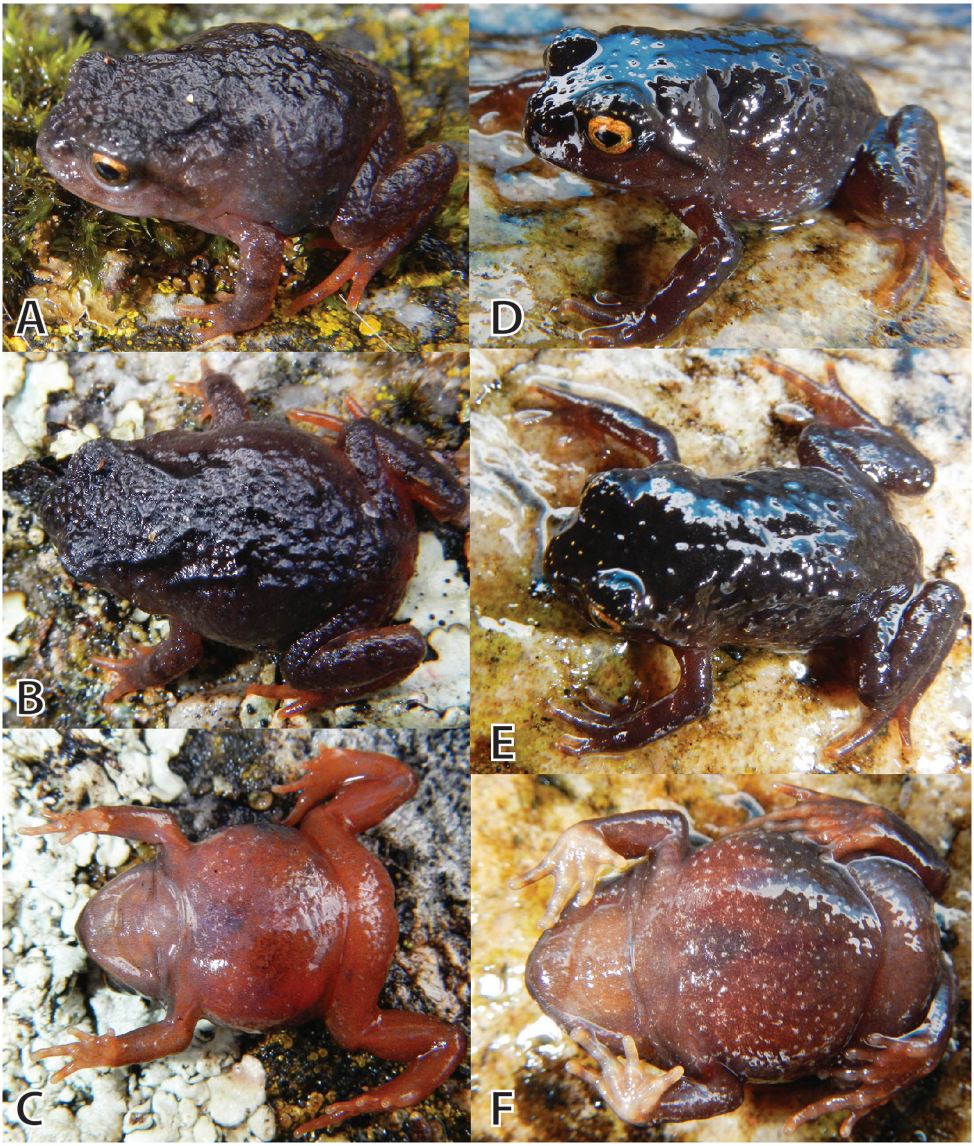

Figure 9. Variation of juvenile paratypes of *Phrynopus inti* sp. n. in dorsolateral, dorsal, and ventral views. **A–C** (MUSM 31969, SVL 16.0 mm), **D–F** (NMP6V 75587, SVL 20.3 mm). Photos by E. Lehr.

2012 at 3609 m a.s.l. (Fig. 10C). The vegetation at the type locality consists of *Polylepis* trees, small bushes, ferns, moss, and Peruvian feather grass. No sympatric anurans were recorded. One specimen (MUSM 31203) was found in the afternoon under moss in a *Polylepis* forest patch near the trail from Tasta to Tarhuish at 3886 m a.s.l. Three specimens (MUSM 31968, 31969, UMMZ 245220) were collected in the morning under rocks and in moss in the mountain slopes of the Toldopampa valley close to Toldopampa

Figure 10. Type locality and habitats of *Phrynopus inti* **sp. n.** Satipo-Toldopampa Road at km 134 on left side of street coming from Satipo, 3350 m a.s.l., 23 June 2013 (**A**); Quebrada Toldopampa, 3670 m a.s.l., 22 June 2013 (**B**); Type locality, Quebrada Tasta, 3609 m a.s.l., 20 May 2012 (**C**); Antuyo, PPPF, 3700 m a.s.l., 27 June 2013 (**D**); Laguna Sinchon, PPPF, 3890 m a.s.l., 29 June 2013 (**E**). Photos by E. Lehr.

at 3670 m a.s.l. (Fig. 10B). Specimens were found under rocks and in moss. Sympatric anurans include *Gastrotheca griswoldi* Shreve, 1941. One specimen (NMP6V 75584) was collected under moss in the early afternoon at the Satipo-Toldopampa Road at km 134 on the left side of the road coming from Satipo at 3350 m a.s.l. (Fig. 10A). Sympatric anurans here include *Pristimantis bounides* (MUSM 31970, 31971) and *Gastrotheca griswoldi* (MUSM 31972). Three specimens (MUSM 31974, 31976, NMP6V 75585) were found under rocks and in moss in Antuyo at 3700 m a.s.l. (Fig. 10D). Sympatric anurans here include *Pristimantis attenboroughi* (MUSM 31975) and *Gastrotheca griswoldi* (IWU 290). Four specimens (MUSM 31984, 31985, NMP6V 75586, 75587) were found in the puna in the afternoon in moss close to the Laguna Sinchon at 3890 m a.s.l. (Fig. 10E). Sympatric anurans here include *Pristimantis puipui* (MSUM 31981–83).

One male specimen (MUSM 31203) had as ectoparasites five trombiculid mites on the right side in the area of the upper arm insertion. Such parasites are not uncommon in Andean frogs (e.g., Quinzio and Goldberg 2015, Lehr et al. 2017).

The IUCN Red List criteria (IUCN 2001) consider that if a species occurs in fewer than 10 threat-defined locations and the extent of occurrence (EOO) is < 20,000 km^2, it should be classified as Vulnerable or Endangered. *Phrynopus inti* sp. n. is known from six localities distributed in the PPPF and its buffer zone (Fig. 10), with an estimated EOO of 101.3 km^2. As such, this new species might be classified as Vulnerable if we take into account these criteria. However, given that the PPPF may host a greater number of locations (two of them are inside the protected area), we propose that *Phrynopus inti* sp. n. should likely be categorized as Near Threatened (NT). Despite that two locations of the known distribution of *Phrynopus inti* sp. n. are within the PPPF (Fig. 10) and formally protected, other factors such as fungal infections, climate change, pollution, and man-made fires (used to expand grazing areas for livestock) continue to be threats for many Andean amphibians even inside protected areas (Catenazzi and von May 2014). Agriculture and cattle raising are more acute in the Toldopampa valley than in the Tasta valley.

Discussion

With a snout-vent length of up to 40.4 mm, *Phrynopus inti* sp. n. represents one of the largest species of the genus. Usually, *Phrynopus* species are characterized by a small robust body, short limbs, narrow or only slightly expanded tips of toes and fingers, and absence of a tympanum. These morphological features seem to be associated with a life in moss layers and grass bunches at elevations between 2600 and 4400 m a.s.l. (Rodríguez and Catenazzi 2017, Duellman and Lehr 2009). In the PPPF, however, this niche is widely occupied by several small *Pristimatis* species (*Pristimantis attenboroughi, P. bounides, P. humboldti,* and *P. puipui*), all of which exhibit a similar body form and lifestyle as most species of *Phrynopus*. In particular, two species of *Pristimantis* in the PPPF, *P. attenboroughi, P. puipui*, appear to have adapted to similar niches in upper montane forests and puna that are typically occupied by species of *Phrynopus* with small robust bodies, short limbs, and discs without circumferential groves. Additionally, like in most species of *Phrynopus*, both *P. attenboroughi* and *P. puipui* lack a tympanum. The use of genetic characters in such cases of convergence is necessary to determine the proper generic placement and phylogenetic relationships (Lehr and von May 2017, Lehr et al. 2017). The inclusion of *P. juninensis* from its type locality in our phylogeny (Fig. 2) revealed the existence of a cryptic species (*Phrynopus* sp.) that was previously thought to be *Phrynopus juninensis*. This new species, which is found in an area located >50 km away from the type locality of *P. juninensis*, will be described in the near future.

Our phylogenetic analysis suggested that *Phrynopus nicoleae*, Chaparro, Padial & De la Riva, 2008 is a junior synonym of *Phrynopus tribulosus* Duellman & Hedges, 2008. The high genetic similarity between *P. nicoleae* and *P. tribulosus* was originally identified by De la Riva et al. (2017), who suggested a possible synonymy, but no formal taxonomic action was proposed. Additionally, new evidence suggests that one other species (not included in the tree presented here) is also genetically similar to both *P. nicoleae* and *P. tribulosus* (von May, unpublished). The synonymy among these three species will be discussed in more detail in an upcoming paper.

De la Riva et al. (2017) pointed out an underestimated radiation of craugastorid frogs in the Eastern Andes of Peru and Bolivia and described five new species and a new genus (*Microkayla*). Ten years earlier, De la Riva (2007) described 12 new species from Bolivia and new amphibians are discovered in similar quantities from Andean Peru. The Andes are indeed a hotspot for biodiversity (Myers et al. 2000); five of the six anuran species recorded by us in upper montane and puna habitats of the PPPF represented new species (see Lehr and von May 2017, Lehr et al. 2017 and this paper), and descriptions of other new anuran as well as reptile taxa are expected. Herpetological surveys conducted by us between 2012 and 2014 demonstrate that the PPPF houses unique amphibian assemblages associated with cloud forest and puna habitats. Therefore, the protection of the PPPF and its native flora and fauna in central Andean Peru is of great importance. The beneficial role of any protected area stands out in light of ongoing habitat loss caused by development and land use changes in neighboring areas including the buffer zone surrounding the PPPF.

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Appendix I

Comparative specimens examined

Phrynopus barthlenae: Peru: Huánuco: ca. 15 km SE Maraypata, near Laguna Gwengway, 3680 m: MUSM 20606 (holotype).

Phrynopus bufoides: Peru: Pasco: La Victoria, 4100 m: MUSM 18074 (holotype), Paucartambo: Río Gayco, 10°49'9.211"S, 75°58'56.21"W, 4345 m: MUSM 32084.

Phrynopus curator: Yanachaga-Chemillén National Park (Sector San Daniel), 3000 m: MUSM 31106 (holotype).

Phrynopus daemon: Peru: Huánuco: Distrito de Churubamba, Cordillera de Carpish, Unchog elfin forest, 3341 m: MUSM 32747 (paratype).

Phrynopus interstinctus: Peru: Huánuco: Cordillera de Carpish, San Marcos, 3100 m: MUSM 29543 (holotype), 3160 m: MUSM 29544–29545 (paratypes).

Phrynopus juninensis: Peru: Junín: road between Cachiyacu and Hacienda Cascas (11°12'43.1"S, 75°35'31.9"W), 3508 m: MUSM 33258.

Phrynopus kauneorum: Peru: Huánuco: Chaglla, Palma Pampa, 3020 m: MUSM 20459 (holotype), MUSM 19894, 20700; Huánuco: Carpish de Moyobamba: MUSM 18585.

Phrynopus peruanus: Peru: Junín: Puna of Maraynioc (11°21'35.2"S, 75° 28'52.6"W), 3825 m: MHNSM 19977–78.

Appendix II

Primers used in this study

Locus	Primer		Sequence (5'-3')	Reference
16S	16SAR	F	CGCCTGTTTATCAAAAACAT	Palumbi et al. (1991)
	16SBR	R	CCGGTCTGAACTCAGATCACGT	Palumbi et al. (1991)
12S	L25195	F	AAACTGGGATTAGATACCCCACTA	Palumbi et al. 1991
	H2916	R	GAGGGTGACGGGCGGTGTGT	Palumbi et al. 1991
COI	dgLCO1490	F	GGTCAACAAATCATAAAGAYATYGG	Meyer et al. (2005)
	dgHCO2198	R	TAAACTTCAGGGT GACCAAARAAYCA	Meyer et al. (2005)
RAG1	R182	F	GCCATAACTGCTGGAGCATYAT	Heinicke et al. (2007)
	R270	R	AGYAGATGTTGCCTGGGTCTTC	Heinicke et al. (2007)
Tyr	Tyr1C	F	GGCAGAGGAWCRTGCCAAGATGT	Bossuyt and Milinkovitch (2000)
	Tyr1G	R	TGCTGGGCRTCTCTCCARTCCCA	Bossuyt and Milinkovitch (2000)