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Molecular Phylogeny, Species Delimitation and Taxonomic Revision of the Australian Spider Wasp Genus *Heterodontonyx* Haupt, 1935 (Hymenoptera: Pompilidae)

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Abstract

Heterodontonyx (Pompilidae: Pepsinae) is an understudied genus with Australasian distribution and most species are endemic to Australia. There have recently been some taxonomic changes involving the genera *Heterodontonyx* and *Cryptocheilus* based on molecular and morphological evidence, however, phylogenetic relationships within *Heterodontonyx*, species delimitation and formal revision have not been conducted. Here, we construct a Maximum Likelihood phylogeny estimate of *Heterodontonyx* based on ITS1, 5.8S, ITS2 region of 30 samples representing seven *Heterodontonyx* morphospecies. bPTP species delimitation approach was employed and ultimately the taxonomic revision of the genus was carried out. Phylogenetic analyses strongly support the monophyly of *Heterodontonyx* and the species delimitation method recognizes eight species among which one new species is identified.

Keywords

Pompilidae Taxonomy, Australian Pomplids, Phylogenetics

1. Introduction

Pompilidae Latreille, 1805, commonly known as spider wasps or spider-hunting wasps, are a family of the order Hymenoptera (Superfamily Pompiloidea).There are five subfamilies within pompilid wasps [1] three of which (Pompilinae, Ceropalinae and Pepsinae) have Australasian distribution. Pepsinae of Australia are divided into the tribes Pepsini and Ageniellini and the Pepsini genus *Heterodontonyx* Haupt, is distributed in New Guinea, Australia, New Caledonia, and

New Zealand [2]. Recently, molecular, and morphological data suggested some taxonomic changes involving the genera *Heterodontonyx* Haupt and *Cryptocheilus* Panzer that warranted taxonomic revision of both genera (Chavoshi, M. *et al*, 2024, submitted). In this study, we utilized both molecular and morphological data to examine phylogeny and specific diversity of *Heterodontonyx* species and revise the genus. There are certain evidence for host shifts in spider wasps which are diversification contributing factors in this group [3].

2. Material and Methods

2.1. Taxon Sampling, DNA Extraction, Library Preparation, Pooling, and Sequencing

A total of 30 specimens covering almost all *Heterodontonyx* species (*H. solomonis* Turner and *H. erythroura* (Cameron) were not included in the phylogeny due to DNA library sequencing failure) included as in group in addition to one out group (POM044 in **Figure 1**). The material was identified to species level using the identification keys developed based on the species descriptions and careful specimen examination. One to three legs of adult spider wasps were cleaned and homogenized for proteolysis on the first day of extraction. Silica-column (Zymo product-Spin Columns II C-Cat No: 1920-050) were used on the second day to extract genomic DNA using the QIAGENDNeasy Blood & Tissue Kit (Cat No: 69504) as per manufacturer's instruction. The purified DNA was resuspended in 25 ul of Tris-HCl 1 mM and stored at 4˚C. DNA quantification was carried out using Invitrogen Qubit dsDNA HS Assay Kit with Fluorometer Denovix DS-II followed by determination of DNA fragment length using Agilent HS Genomic DNA Kit DNF-488 with 12 Capillary Fragment Analyzer System (Advanced Analytical Technologies, Inc.). DNA library building was achieved using NEBNex Ultra II DNA Library Prep Kit for Illumina (Cat No: E7645) with 3 - 15 amplification cycles depending on the DNA input. As the final step, libraries were eluted in Tris-HCl 1 mM to reach equimolar concentration of 2 nM followed by post-PCR clean-up of the pooled libraries using 1× magnetic bead ratio (NEBNext Sample Purification Beads). Lastly, 25 - 200 ul of the pooled, cleaned, single-indexed (using NEBNext Multiplex Oligos for Illumina) libraries was submitted for whole-genome shotgun sequencing in one lane of NextSeq 550 System 300 cycles (paired end reads) at the ACRF Biomolecular Resource Facility (https://jcsmr.anu.edu.au/).

2.2. Data Processing, Sequence Alignment, Phylogenetic Assessment, and Species Delimitation

Raw reads were cleaned and trimmed with Trimmomatic [4] and quality checked with FastQC (Babraham Bioinformatics). The resulting trimmed reads were de-novo assembled using Trinity v2.1.1 [5]. ITS1, 5.8S, ITS2 reference sequences were obtained by mapping POM334 to a 5.8S sequence (accession no. X89481) from [6] with 25 iterations and was then used to as the reference se-

quence to extract ITS1, 5.8S, and ITS2 from assembled contigs. Phylogenetic analyses were carried out on the ITS dataset under maximum likelihood (ML). For ML analyses, we used IQ-TREE 1.7.0 [7] with Model Finder [8] and ultrafast bootstrap [9]. The phylogenetic tree was visualized in Figtree v.1.4.1 (http://tree.bio.ed.ac.uk/software/Figtree/). ITS matrix was then used to examine delimitation scheme with PTP and bPTP on the server (https://species.h-its.org/).

2.3. Taxonomic Revision of *Heterodontonyx* Species

Where possible, images of the Type material of each species were included and as many non-type material as possible were examined using a Leica S7 APO dissecting microscope. Images were taken at the Australian National Insect Collection (Canberra, ACT 2601 Australia) using a Canon EOS 7D Mark II DSLR with Visionary Digital Big Kahuna (Bk) Camera system using 65 mm (Canon lens MP-E65mmf/2.8 1-5x Macro) and 100 mm (Canon lens EF 100 mm f/8 L IS USM), processed using Helicon focus Stacker and edited with Photoshop CS5. Specimens were examined from the following collections: Australian Museum, Sydney, Australia (AM); Australian National Insect Collection (ANIC); Humbolt University Zoologischen Musuem (HUM); Museo Civico di Storia Naturale "Giacomo Doria", (MCG); Museum Victoria (MV); Natural History Museum (BMNH); Queensland Museum (QM); South Australian Museum (SAM); and Western Australian Museum (WAM). Morphological terminology used here follows Harris 1987 and wing terminology follows Day 1988.

3. Results

3.1. Phylogenetic Analysis and Species Delimitation

The IQ-TREE analyses overall yielded well supported interspecific relationships within *Heterodontonyx* (**Figure 1**). *Cryptocheilus fulvus* was used as outgroup and the in group (node A) is split in two branches B and C. Based on bPTP results, branch B holds five species and branch C contains three species. ML tree topology suggests that branch B is sister to group C which proposes the following phylogenetic estimates: *H. tuberculatus* (shown in yellow in **Figure 1**) is sister to a group containing *H. bicolor*, *H. fulvidorsalis*, *H. darwinii* and a new species (node D in **Figure 1**). POM 168 on **Figure 1**, the molecular new species for which the morphological description follows in the next section, is sister to node E containing *H. darwinii*, *H. fulvidorsalis* and *H. bicolor*. *H. darwinii* is sister to *H. fulvidorsalis* + *H. bicolor* (node F in **Figure 1**). *H. fulvidorsalis* (shown in brown in **Figure 1**) is sister to *H. bicolor* (shown in red in **Figure 1**). In addition, the phylogeny suggests that *H. australis* (shown in blue in **Figure 1**) is sister to a group containing *H. distinctus* and *H. praepositus* (node G in **Figure 1**) and that *H. distinctus* (shown in green in **Figure 1**) is sister group to *H. praepositus* (shown in purple in **Figure 1**).

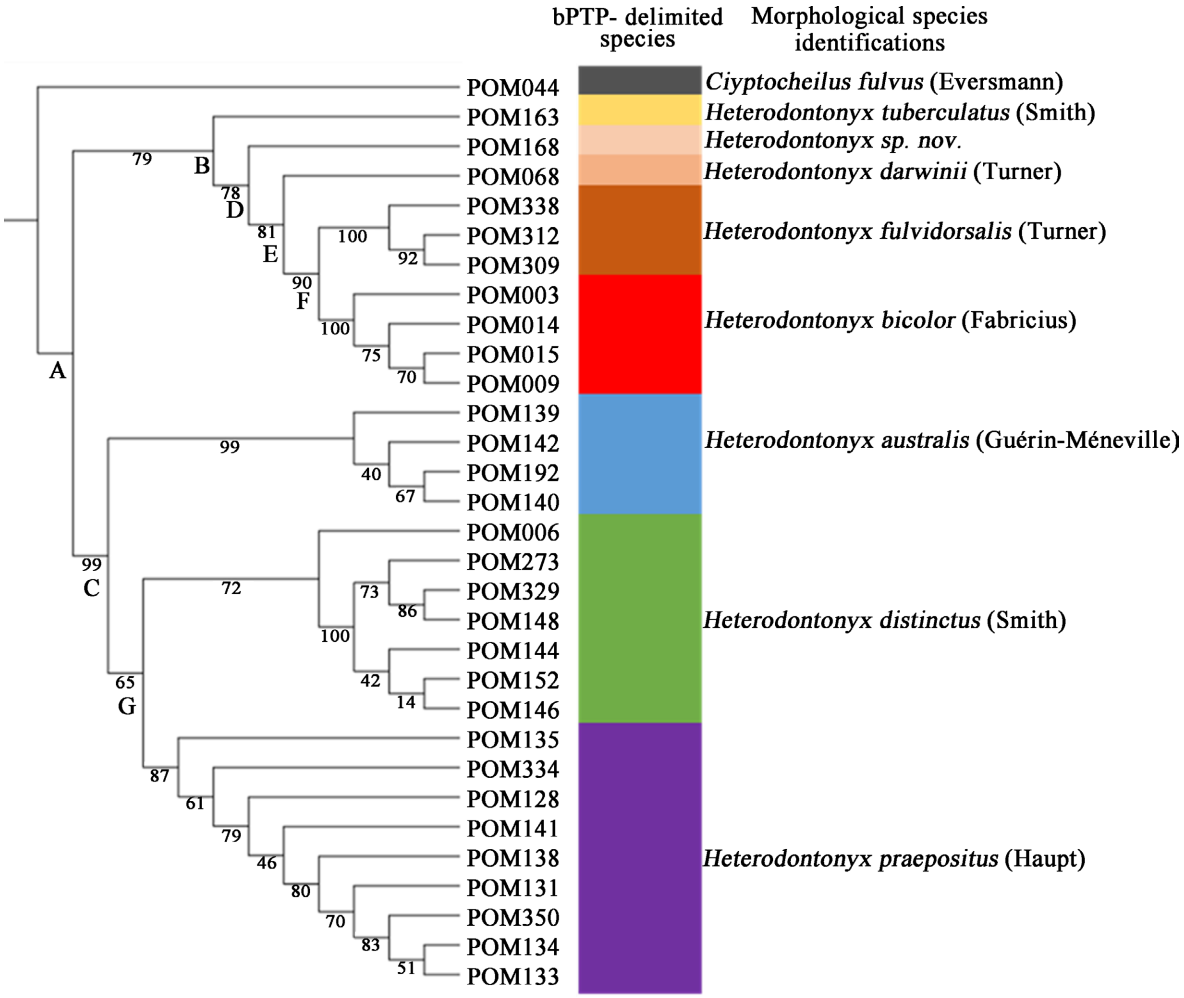

Figure 1. Maximum Likelihood tree reconstruction of *Heterodontonyx* based on the molecular information of ITS1, 5.8S, ITS2 region. Statistical support values of Ultra-Fast Bootstraps are shown on each node. bPTP suggested delimitation scheme of molecular units shown on the right panel next to their morphological identification.

3.2. Taxonomic Revision of the Australian Spider Wasp Genus *Heterodontonyx* Haupt, 1935 with Description of a New Species, Revised Key, New Records and a Host Association

Systematics of the genus Heterodontonyx *Haupt* 1935.

Heterodontonyx Haupt, 1935. Type species: *Heterodontonyx basalis* Haupt, 1935 (**Figure 2**) by subsequent designation, see Banks, 1941:234 and Pate, 1946: 90 (=*Sphex bicolor*, synonymy by Wahis [10].

Diagnosis

Black and orange wasps of small to large size (10 - 40 mm) with golden-yellow wings; clypeus medium to large and convex, with labrum concealed to completely exposed; antennal segments slender and elongate; propodeum black or reddish-yellow, rugose, with or without tubercules; vein 2rs-m straight to slightly curved, 1m-cu vein reaching the second submarginal cell (SMC2) slightly to moderately beyond its middle; marginal cell elongated, ratio of the inter-tegular distance to the length of the second abscissa of forewing vein Rs

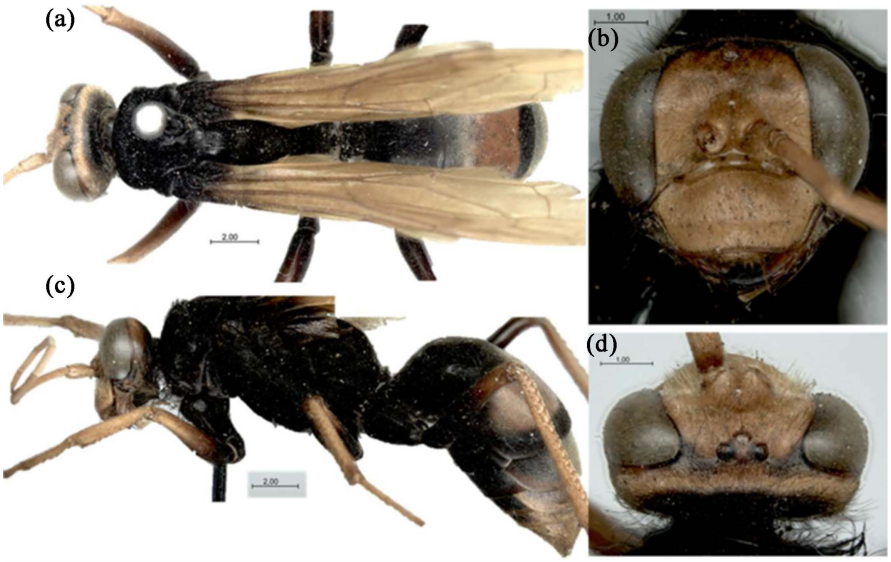

Figure 2. (a)-(d) *Heterodontonyx basalis* female lectotype (a) dorsal view (b) head, frontal view, (c) lateral view, left side (d) head, dorsal view, scale bars: (a), (c): 2 mm, (b), (d): 1 mm. Images taken by Lars Krogmann from HUM.

(ITD: SaRs) ranges from 1.5 to 2.5. Female metatibia serrated with spines.

Key to *Heterodontonyx* Species

The key is based on both sexes, but caution should be taken as in a few cases only one sex is known (*H. erythroura*, *H. solomonis* and *H. wahisi*). Despite measurable sexualdimorphism in some Pompilidae (e.g., *Aplochares imitator* (Smith)), our observations suggest that, apart from genitalia, body size, size of black area on the head, relative length of first to second flagellar segment and occasional bifid tarsal claws in males, the sexes of *Heterodontonyx* are not distinctly dimorphic.

1. a. Head, mesosoma and metasoma black ... *H. solomonis* Turner (**Figure 10**)
   b. Body black and orange/yellow/reddish-yellow 2
2. a. Sides of propodeum rounded; body size small (10 - 20 mm) 3
   b. Full tubercles or half tubercles on sides of propodeum 4
3. a. Body with black setae; size 10 - 15 mm 5
   b. Body bare, without long setae; second metasomal segment sometimes with apical black band ... *H. australis* (Guérin-Méneville, 1838) (**Figure 3**)
4. a. Full tubercles on sides of propodeum 6
   b. Half tubercles on sides of propodeum; prothorax and mesothorax brown yellow *H. fulvidorsalis* ..... (Turner, 1910) (**Figure 8**)
5. a. Female head entirely orange, some males with pronotum golden yellow orange, body size 10 - 15 mm ..... *H. distinctus* (Smith, 1868) (**Figure 6**)
   b. Body size 10 - 15 mm, second metasomal segment sometimes with an apical black band ..... *H. praepositus* (Haupt, 1935) (**Figure 9**)
6. a. Clypeus long and narrow (length: width: 1.5 - 1.75); labrum completely Exposed 7

b. Clypeus short and wide (length: width: 2 - 2.5); labrum slightly to moderately exposed 8

7. a. Pubescence moderate; antennae very long and slender; head, pronotum and mesoscutum reddish-yellow brown; slight compression between first and second metasomal segments.... *H. darwinii* (Turner, 1910) (**Figure 5**)

b. Body covered with dense, black, and golden setae; pronotum orange, first metasomal segment and apical second metasomal segment black, remaining metasomal segments orange..... *H. wahisi* sp. nov (**Figure 12**)

8. a. Mesosoma entirely black, second metasomal segment orange ..... *H. tuberculatus* (Smith, 1855) (**Figure 11**)

b. Mesosoma entirely black, second metasomal segment apically or entirely black 9

9. a. Second metasomal segment entirely black ..... *H. erythroura* (Cameron 1906) (**Figure 7**)

b. Second metasomal segment with black basal band..... *Heterodontonyx bicolor* (Fabricius, 1775) (**Figure 4**)

Heterodontonyx australis (Guérin-Méneville, 1838)

Pompilus australis Guérin–Méneville, 1838: 260. Type data: syntypes MCG one male and one female. Type locality: NSW, Sydney (as Port Jackson, Nouvelle-Hollande); Froggatt, 1892: 212 [cat.]; Guiglia, 1948: 178; Guiglia & Pasteels, 1961: 19 [notes on the type (inItalian)]. *Cryptochilus* (*Prionocnemis*) australis Schulz, 1906: 166 [comb. nov., status as senior secondary homonym of *Cryptochilus* (*Prionocnemis*) australis Holmberg, 1903; Schulz, 1911: 115, 207 [note.].

Heterodontonyx australis Haupt, 1935: 309 [comb. nov., desc., Figure.].

Cryptocheilus australis Harris, 1987: 25 [comb. nov., descr., Figures., biol., dist. (New Zealand), notes]; Forster, 1994: 215 [note]; Harris, 1999: 143–158, 223, 226, 229–232 [notes, list, biol., Figures.]. Elliot, 2007: 20 [cat.].

Prey records: *Dolomedes minor* Koch, 1872; *Dolomedes aquaticus* Goyen, 1888; *Dolomedes* spp. (Pisauridae) (Harris, 1999: 157)

Adult food sources: *Leptospermum scoparium* Forst. & Forst. (Myrtaceae); *Pastinaca sativa* L. (Apiaceae) (Harris, 1987: 28 and Harris, 1999: 157); *Gomphocarpus physocarpus* E. Mey. (Asclepiadaceae) (Forster, 1994: 215).

Material examined.

Holotype image:

The male lectotype is from the Guérin collection and determined by Raymond Wahis in1995. The material is pinned on a paper card and in a fair condition, some legs and antennalsegments are missing from both sides. The female paralecto type is from the Guérin collection and determined by Raymond Wahis in 1995. The material is pinned on a paper card and in a fair condition, both eyes, distal segments from left antenna and legs are missing and wings also are slightly torn.

Other material (See **Table 1**):

Length 10 - 20 mm; colour black and orange; body not heavily covered with setae, almost bare; head of female with face and vertex yellow orange, except for a black band as wide as ocellartriangle passing through ocelli and reaching

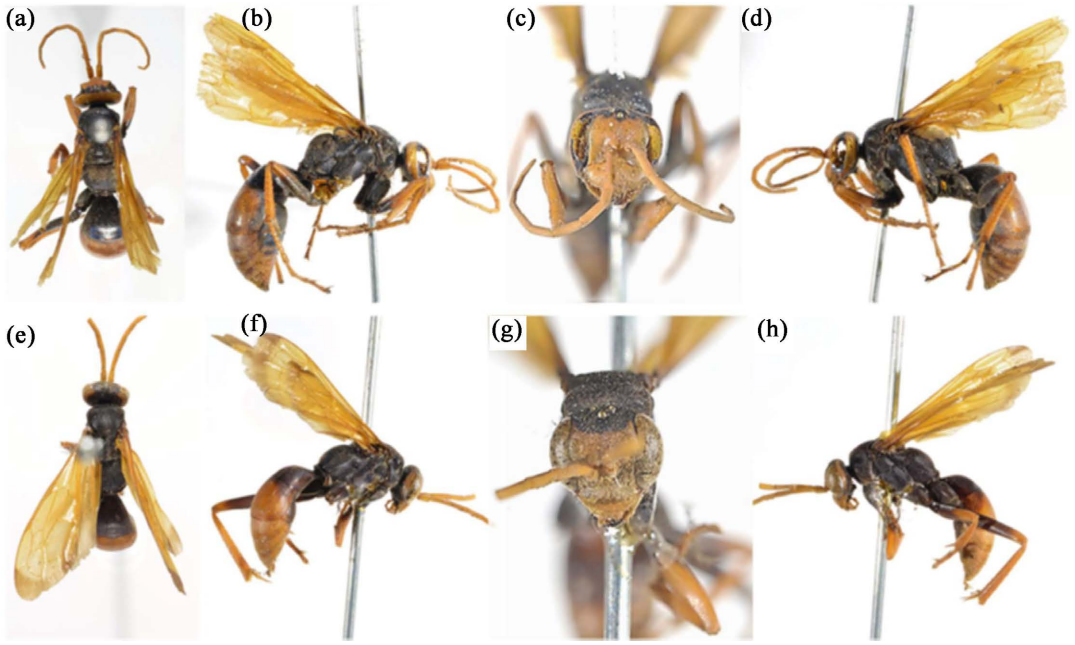

Figure 3. (a)-(d) *Pompilus australis* female paralectotype (a) dorsal view (b) lateral view, right side (c) head, frontal view (d) lateral view, left side (e)-(h) *Pompilus australis* male lectotype (e) dorsal view (f) lateral view, right side (g) head, frontal view (h) lateral view, left side. Images taken by Maria Tavano from MCG.

Table 1. Diagnosis (modified from Harris, 1987).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by	Locality
Female	ANIC32_101009	20 Jun. 1929	NT	18S	135.5E	Campbell, T.G.	NT
Female	ANIC32_100927	16 Feb. 1969	ACT	35.35S	148.8E	Upton, M.S.	ACT
Female	ANIC32_101089	4. Oct. 1969	WA	24.8159S	113.6298E	R.W. Matthews	WA
Female	ANIC 32_099228	Oct. 1972	Qld.	24.87S	152.35E	H. Frauca	Qld.
Female	ANIC32_101024	12. Nov. 1987	SA	34.01S	139.49E	I. Naumann, J. Cardale	SA
Male	ANIC32_115588	22 Feb. 1957	New Caledonia	21.2107S	165.8517E	J. Rageau	New Caledonia
Male	ANIC32_101063	12 Feb. 1970	ACT	35.4735S	149.0124E	Evans, H. & Matthews, R.W.	ACT
Male	ANIC32_099227	3 Jun. 1982	NSW	33.71S	150.38E	Unknown	NSW
Male	TMAG-F6673	18 Dec. 2013	Tas.	42.8680S	147.3854E	S .J. Grove	Tas
Male	ANIC-PO1507	5 Dec. 2017	Qld.	26.1.15S	153.051E	Xuankun Li, David Yeates	Qld.
Male	ANIC-PO1508	19 Feb. 2018	NSW	33.31.17S	150.21.29E	Xuankun Li, David Yeates	NSW
Male	ANIC-PO1506	26 Feb. 2018	NSW	33.31.17S	150.21.29E	Xuankun Li, Alan Lanford	NSW
Male	ANIC-PO1509	26 Feb. 2018	NSW	33.31.17S	150.21.29E	Xuankun Li, Alan Lanford	NSW

compound eyes; head of male with vertex and disc of frons black; propodeum without tubercles; second metasomal segment sometimes with a very narrow, apical black band.

Redescription

Female

Coloration. Head orange yellow except for a narrow area between the eyes, the end of the mandible, and the occipital region, which are dark/black; mesosoma black except for tegula which is orange; tibiae and tarsi orange, femora black basally, orange apically; firstmetasomal segment black, second metasomal segment orange, sometimes with narrow apicalblack band, remainder yellow orange; wings yellow orange, with a narrow apical darkening.

Head. Head wider than long, TFD/FD = 1.2; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.75; frons with median line reaching median ocellus; apical margin of clypeus slightly concave; clypeus rather short, clypeus length: width = 2.27; labrum on same plain as clypeus moderately exposed beneath; malar space very short, almostnon-existent; first flagellar segment slightly longer than the second. Mesosoma.

Mesosoma. Polished with few setae, pronotum relatively short, with a very weak median line, its posterior margin strongly angulate; metanotum knobbed; metapostnotum suppressed; propodeum slightly wrinkled across with median line, without tubercules; dorsal edge of hindtibia with carina bearing spines; tarsal claws dentate. Metasoma. Metasoma polished, pygidium covered by short, abundant setae, metasoma 1.21× length of mesosoma.

Male

Similar to female except differences described here: vertex and most of the frons black; clypeus relatively long; hind tibiae without serration with short spines; body size smaller.

Distribution: NSW, New Zealand (North Island). Tas., WA, Qld. (Elliot, 2007) Newrecords: NT, SA, New Caledonia.

Heterodontonyx bicolor (Fabricius, 1775)

Sphex bicolor Fabricius, 1775: 352. Type data: type BMNH female. Type locality: Australia (as nova Hollandia); Fabricius, 1781: 450 [descr. (in Latin), dist.]; Fabricius, 1787: 277 [descr. (in Latin)]; Gmelin, 1790: 2732 [descr. (in Latin, dist.]; Fabricius, 1793: 217 [descr. (in Latin); dist.]; Zimsen, 1964: 387 [note on type]. *Pompilus bicolor* Fabricius, 1804: 198 [comb. nov.; descr. (in Latin); dist.]; Smith, 1863b: 132 [dist.]; Smith, 1863a: 29 [note, dist.]; Smith, 1871: 353 [cat., dist.]; Schulz, 1906: 169 [as senior secondary homonym of *Pompilus bicolor* (Spinola, 1808)]. *Salius bicolor* Tillyard, 1926: 292 [note]; McKeown, 1942: 185 [note]. *Cryptocheilus bicolor* Evans & Matthews, 1973: 46 [comb. nov., biol.]; Evans 1981: 9 [prey]; Hirst 1992: 365 [prey record]; Williams & Adam 1995: 54 [list]. Elliot, 2007: 20 [cat.].

Prey records: *Isopedellapessleri* (Thorell, 1870) (as *Isopedapessleri* (Thorell)); *Isopeda sp.* (Sparassidae) (Evans & Matthews, 1973: 46-47), *Heteropoda jugulans* Koch, 1876; *Isopedaleishmani* Hogg, 1903 (as *Isopoda leishmani* Hogg)

(Sparassidae); *Lycosa sp.* (Lycosidae) (Evans 1981: 9-10), *Isopedacanberrana* Hirst, 1992 (Heteropodidae) (Hirst, 1992).

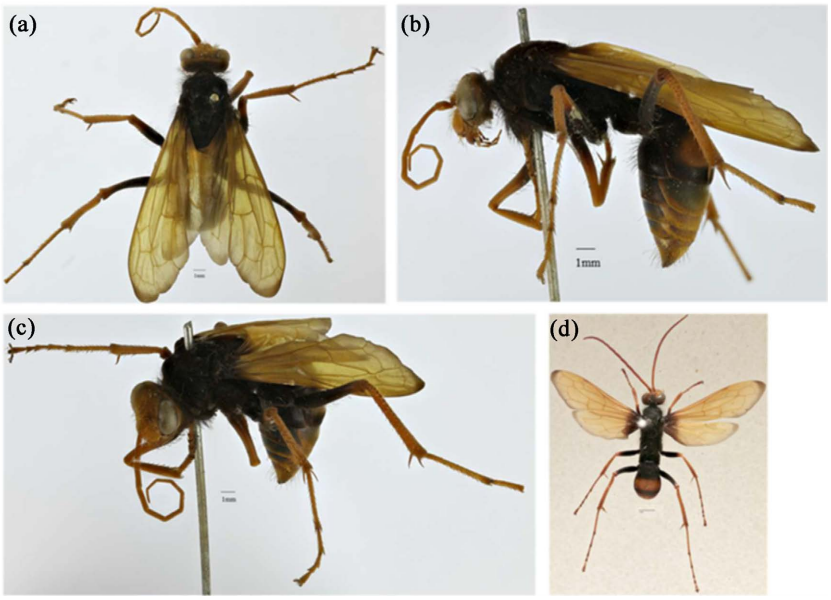

Figure 4. (a)-(c) *Sphex bicolor* female holotype (a) Dorsal view (b) Lateral view, left side (c) Head and fronto-lateral view (d) Non-type male, dorsal view. Scale bars: 1 mm. Images (a)-(c) taken by Xuankun Li in BMNH.

Material examined

Holotype image

Type accession number: BMNH (E) #668328, NHMUK 013380164 holotype is from the Banks collection and is in good condition except that the last tarsal segment of hind legs are missing.

Other material (See **Table 2**):

Length 20 - 40 mm; colour black and orange; body heavily covered in dense black setae; head of female with face and vertex orange, except for a black band between ocelli; head of male with vertex and disc of frons black; propodeum with two distinct tubercles; second metasomal segment with a wide apical black band.

Table 2. Diagnosis (modified from Harris, 1987).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by
Female	QM.No.ENT19.08	10 Jan. 1966	PNG	9.4814S	147.1461 E	E. Mann
Female	ANIC32_100861	5 May. 1981	Vic.	37.9145S	145.1350 E	M. Kotzman
Female	ANIC32_100890	10-12 May. 1981	Qld.	15.29S	145.16E	I. D. Naumann
Female	ANIC32_100862	20 Aug. 1982	NT	18.6S	136E	R. Patterson 4340
Female	ANIC32_100853	22 Aug. 1989	SA	27.54S	135.49E	I. BUNIC
Female	ANIC32_100848	17 Feb. 1986	NSW	33.4622S	151.2561 E	D. B. Mc Corqundale
Male	ANIC32_100837	5 Apr. 1971	WA	21.34 S	117.03E	E. F. Riek
Male	ANIC32_100882	3-14 Feb. 1977	NT	11.01S	136.45E	T. A. Weir

Redescription

Female

Coloration. Head orange yellow except for a narrow area between the eyes, the end of the mandible, and the occipital region, which are dark/black; mesosoma black; tibiae and tarsi orange, femora black basally, orange at apex; first metasomal segment black, second metasomal segment orange with apical black band, remainder yellow orange; wings yellow orange, with a narrow apical and basal darkening. Head. Head wider than long, TFD/FD = 1.16; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.72; frons with median line reaching median ocellus; apical margin of clypeus straight; clypeus rather short, clypeus length: width = 2.2; labrum on same plain as clypeus concealed to slightly exposed beneath; malar space very short, almost non-existent; first flagellar segment clearly longer than the second.

Mesosoma. Setose, pronotum relatively short, with a very weak median line, its posterior margin strongly angulate; metanotum knobbed; metapostnotum suppressed; propodeum wrinkled across with a median line which is more prominent at the posterior ridge, tuberculate; dorsal edge of hind tibia with two rows of spine-bearing scalelike elevations which become less dense towards tarsus, tarsal claws dentate.

Metasoma. Metasoma punctate, pygidium covered by short, abundant setae, metasoma 1.25× length of mesosoma.

Male

Similar to female except differences described here: vertex and disc of frons black; clypeus relatively long; first flagellar segment slightly longer than the second; hind tibiae without serration with short spines; body size smaller.

Remarks

Original description of this species by Fabricius, 1775 was based on one sex only (female).

Distribution: ACT, NSW, QLD, WA, Indonesia, New Zealand (Elliot, 2007). New records: NT, SA, PNG, Vic.

New host association: *Isopedellaleai* (Hirst) loan from SAM accession number: 32-42650.

Heterodontonyx darwinii (Turner, 1910)

Cryptocheilus darwinii Turner, 1910: 318. Type data: type BMNH one male and one female.

Type locality: NT, Darwin. Elliot, 2007: 21 [cat.]

Material examined

Holotype co-type male (accession number: NHMUK 013380165) and holotype female. The male cotype is pinned on a paper card and in a very good condition. The holotype material is also pinned and is in good condition except for the broken left antennae.

Other material (See Table 3):

Length 30 - 40 mm; colour black and brown-yellow; body not heavily covered with setae; head of female brown-yellow; head of male with vertex backwards

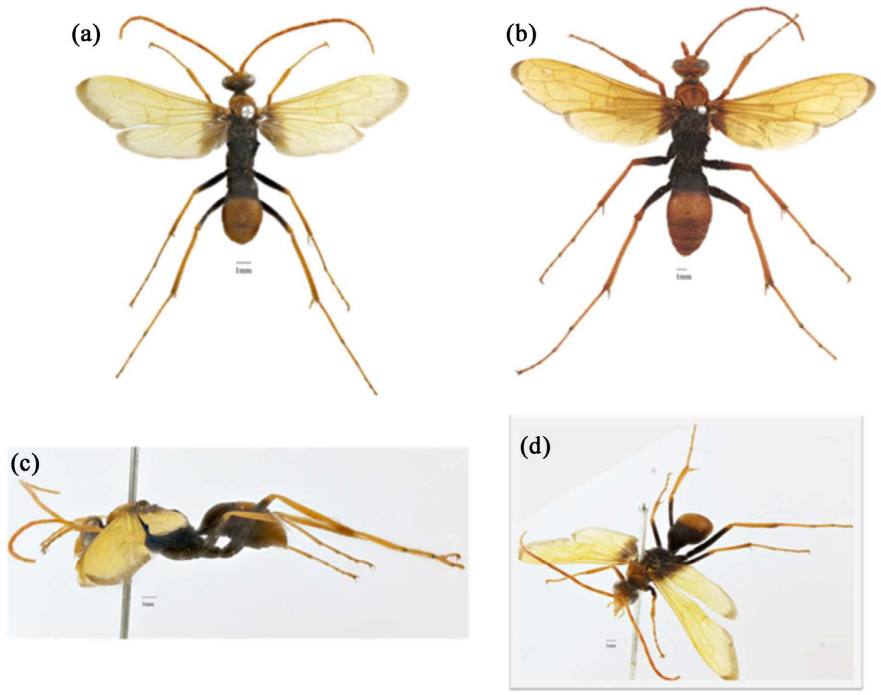

Figure 5. (a)-(d) *Cryptocheilus darwinii* (a) Male co-type, dorsal view (b) Female holotype, dorsal view (c) Male co-type, lateral view, left side (d) Male co-type, head and fronto-dorsal view. Scale bars: 1 mm. Images (a), (c), (d) taken by Xuankun Li in BMNH.

Table 3. Diagnosis (modified from Turner 1910).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by
Female	QMENT19.08	Unknown	Qld.	16.9203S	145.7710E	F. P. Dodd
Male	ANIC	Oct. 1980	Qld.	14.17S	144.12E	L. Taylor

black; pronotum and mesoscutum brown-yellow; propodeum with two distinct tubercles; first metasomal segment black with apical constriction.

Redescription

Female

Coloration. Head brown-yellow; mesosoma black except for tegula, pronotum and mesoscutum which are brown-yellow; tibiae and tarsi brown-yellow, femora black baslly, brown-yellow apically; first metasomal segment black, second metasomal segment onwards brown-yellow; wings yellow orange, with narrow apical and basal darkening.

Head. Almost the same width as length, TFD/FD = 1.05; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.77; frons with median line reaching median ocellus; apical margin of clypeus slightly concave; clypeus rather long, clypeus length: width = 1.25; labrum on same plain as clypeus moderately exposed beneath; malar space very short, almost nonexistent; antenna very long and slender; first flagellar segment slightly longer than the second.

Mesosoma. Mesosoma with moderate pubescence; pronotum relatively short, with an obvious median line, its posterior margin strongly angulate; metanotum

knobbed; metapostnotum suppressed; propodeum wrinkled across with a median sulcus, tuberculate. spine-bearing dorsal edge of hind tibia moderately serrated; tarsal claws dentate.

Metasoma. Metasoma polished, softly punctate, pygidium covered by short, golden set ae, metasoma 1.14× length of mesosoma.

Male

Similar to female except differences described here: vertex black; clypeus longer; first flagellar segment slightly longer than the second; hind tibiae without serration with short spines; body size slightly smaller.

Distribution: NT. New records: QLD

Heterodontonyx distictus (Smith, 1868)

Pompilus distinctus Smith, 1868: 242. Type data: type BMNH, male. Type locality: A, Champion Bay; Froggatt, 1892: 212 [cat.].

Cryptocheilus distinctus Evans *et al.* 1981: 10 [prey and nest]. Elliot, 2007: 21 [cat.].

Prey records: *Eriophora biapicata* (Koch, 1871) (Araneidae); *Lycosalaeta* Koch, 1877 (Lycosidae) (Evans, 1981: 10).

Material examined

Holotype

Type accession number: B.M. TYPE HYM. 19.156, NHMUK010577193, 68-6,

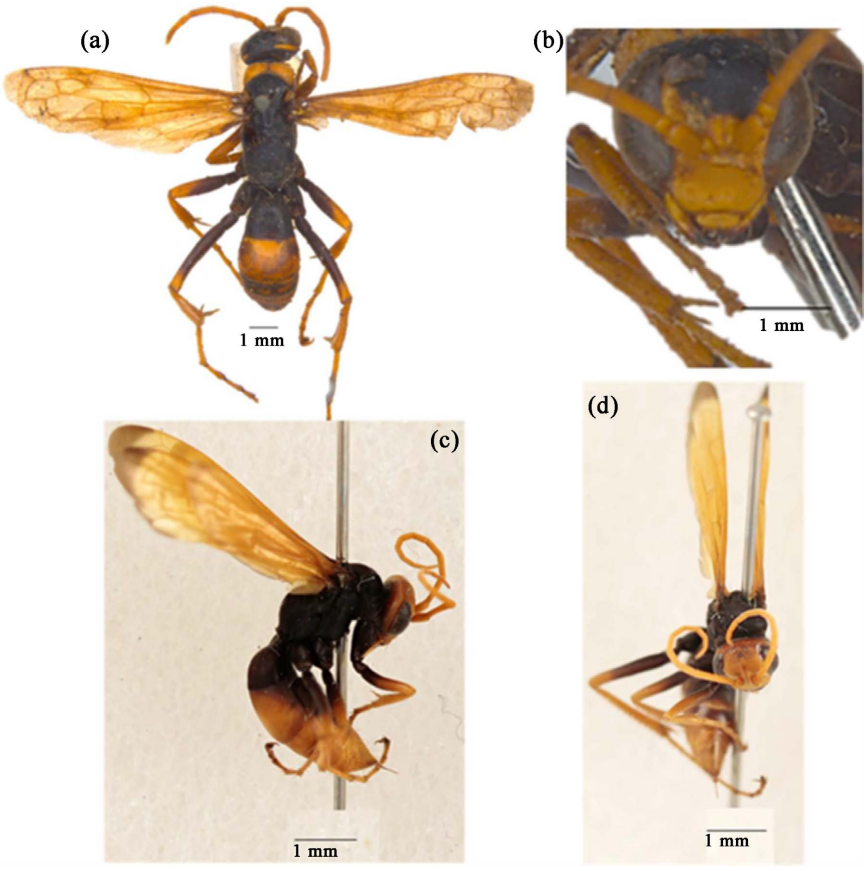

Figure 6. (a), (b) *Pompilus distinctus* male holotype (a) Dorsal view (b) Head, frontal view (c), (d) Female non-type (c) lateral view, right side (d) head, frontal view. Scale bars: 1 mm.

The type is determined by R. Wahis in 1995, is pinned and is in fair condition, lower right part of the right forewing is torn, and the right hind wing is broken and missing for the most part, the lasttarsal segment of the right hind leg is missing, and left antennae has some distal brokensegments.

Other material (See Table 4):

Length 10 - 15 mm; colour black and orange; body moderately setose; head of female entirely orange; head of male with vertex and disc of frons black; some males with pronotum golden; propodeum without tubercles; second metasomal segment without any apical black band.

Redescription

Female

Coloration. Head orange, mesosoma black; tibiae and tarsi orange, femora black basally, orange at apex; first metasomal segment black, second metasomal segment onward orange; wings yellow orange, with a narrow apical darkening.

Head. Head wider than long, TFD/FD = 1.2; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.86; frons with median line reaching median ocellus; apical margin of clypeus straight; clypeus medium, clypeus length: width = 2; labrum on same plain as clypeus slightly exposed beneath; malar space very short, almost non-existent; first flagellar segment about the same length as the second.

Mesosoma. Bears black setae; pronotum relatively short, with a median line, its posterior margin angulate; metanotum knobbed; metapostnotum suppressed; propodeum wrinkled across with a median line, without tubercules; dorsal edge of hind tibia serrate with spines; tarsal claws dentate.

Metasoma. Metasoma polished, sparsely punctate, pygidium covered by short, abundant golden setae, metasoma 1.16× length of mesosoma.

Male

Similar to female except differences described here: vertex and most of the frons black; hind tibiae without serration with short spines; body size slightly smaller.

Remarks

Original description of this species by Smith, 1868 was based on one sex only (male).

Table 4. Diagnosis (modified from Smith, 1868).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by
Female	MUS.VICENTO2019-HYM-62732	27 Mar. 1949	VIC	35.5789S	143.7749E	A. N. Burns
Female	ANIC32_101162	18-22 Feb. 1970	VIC	35.7678S	142.0545E	H. E. Evans, R. W. Matthews
Female	ANIC32_101166	Oct. 1971	QLD	24.87S	152.3489E	H. Frauca
Male	ANIC32_101154	3-6 Feb. 1970	QLD	23.1335S	150.7374E	H. E. Evans
Male	ANIC32101060	21-22 Feb. 1970	VIC	36.1S	142E	Evans, H., Matthews, R. W.
Male	ANIC32_101134	Oct. 1971	QLD	24.87S	152.35E	Frauca, H.
Male	WAMReg. No. E101033	1 Apr. 1980	SA	31.82S	138.59E	Bohart, R. M.

Distribution

NSW, WA. (Elliot, 2007). New records: Qld., Vic., SA

Heterodontonyx erythroura (Cameron 1906)

Saliuserythroura Cameron 1906. Type data: Type depository unknown, female, Type locality: Lake Sentani

Material examined

One non-type female specimen studied Accession number: BM O.I.E.Coll.A 5723; collected in 07. Oct. 1968 by F.R.Wylie in Bulolo Morabe province, PNG

Diagnosis (modified from Cameron 1906).

Length 35 mm; colour black and orange; body heavily setose; head of female with vertex black and disc of frons orange; propodeum with two distinct tubercles; second metasomal segment black.

Redescription

Female

Coloration. Head orange except for vertex backwards and the end of the mandible which are dark/black; mesosoma black; tibiae and tarsi orange; femora

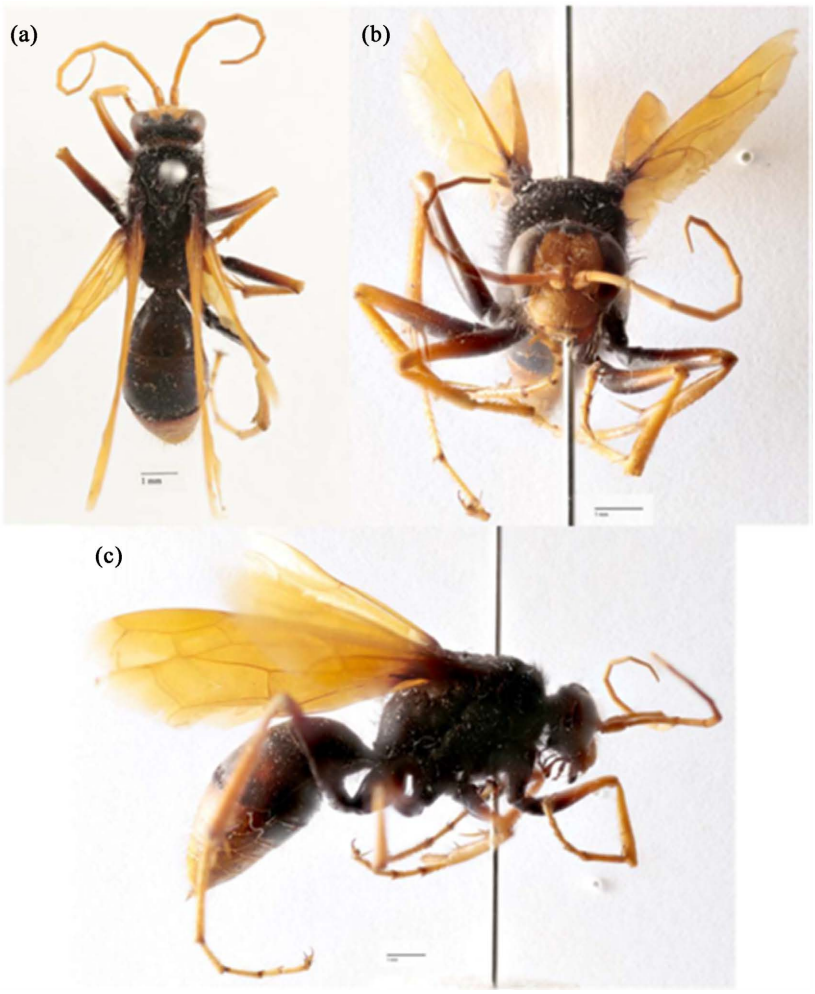

Figure 7. (a)-(c) *Heterodontonyx erythroura* female non-type (a) Dorsal view (b) Head, frontal view (c) Lateral view, right side. Scale bars: 1 mm.

black basally, orange apically; first and second metasomal segments black; third metasomal segment onward orange; wings yellow orange, with a narrow apical darkening. Head. Head slightly wider than long, TFD/FD = 1.1; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.75; frons with median line reaching median ocellus; apical margin of clypeus straight; clypeus slightly long, clypeus length: width = 1.94; labrum on same plain as clypeus moderately exposed beneath; malar space very short, almost non-existent; first flagellar segment clearly longer the second. Mesosoma. Setose, pronotum relatively short, with a very weak median line, its posterior margin convergent towards the median line; metanotum knobbed; metapostnotum suppressed; propodeum wrinkled across without a median line, tuberculate; dorsal edge of hind tibia with spine-bearing elevations; tarsal claws dentate.

Metasoma. Metasomasetose, punctate, pygidium covered by short, abundant setae, metasoma 1.2× length of mesosoma.

Male

Unknown.

Distribution: Bulolo, PNG.

Heterodontonyx fulvidorsalis (Turner, 1910).

Cryptocheilus fulvidorsalis Turner, 1910:319. Type data: type BMNH, female. Type locality: QLD, Mackay. Elliot, 2007: 21 [cat.].

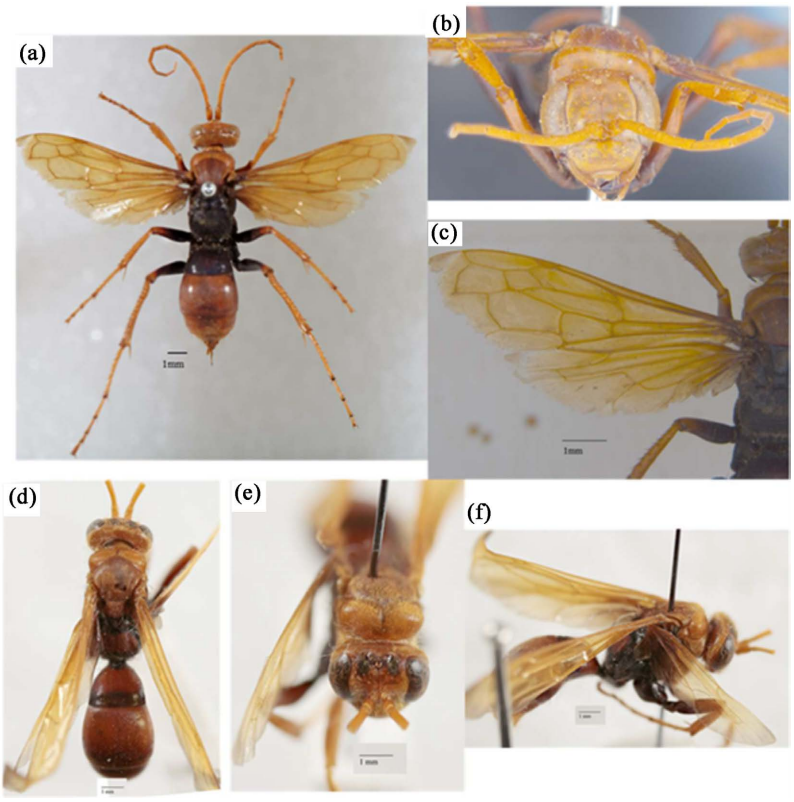

Figure 8. (a)-(c) *Cryptocheilus fulvidorsalis* female holotype (a) Dorsal view (b) Head, frontal view (c) Left fore and hind wings (d)-(f) Non-type male (d) Dorsal view (e) Head, fronto-dorsal view (f) Lateral view, right side. Scale bars: 1 mm.

Material examined

Holotype

Type accession number: B.M. TYPE HYM. 19.155, NHMUK010577201 from Turner Collection with the accession number 1910-7. Type is female, pinned, in very good Condition.

Other material (See Table 5):

Length 15 - 25 mm; colour brown-yellow and black; body moderately covered in golden setae; head of female entirely brown-yellow; head of male brown yellow with a black area in vertex; pronotum and mesoscutum brown-yellow; propodeum with two half-tubercles; propodeum black in female, brown-yellow in male; first metasomal segment black in female, brown-yellow with apical darkening in male.

Redescription

Female

Primarily based on holotype

Coloration. Head brown-yellow; mesosoma brown-yellow (pronotum, tegula and mesoscutum) and black (scutellum and propodeum); tibiae and tarsi brown-yellow, femora black basally, brown-yellow apically; first metasomal segment black, second metasomal segment onward brown-yellow.

Head. Head slightly wider than long, TFD/FD = 1.12; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.83; frons with median line reaching median ocellus; apical margin of clypeus slightly concave; clypeus medium, clypeus length: width = 2; labrum on same plain as clypeus slightly exposed beneath; malar space very short, almost non-existent; first flagellar segment slightly longer the second.

Mesosoma. Moderate pubescence, pronotum relatively short, with a clear median line, its posterior margin convergent towards median line; metanotum without knob; propodeum wrinkled across with a very weak median line, without any prominent tubercles (half-tuberculate); dorsal edge of hind tibia with spine-bearing tooth-like elevations; tarsal claws dentate.

Metasoma. Metasoma polished, sparsely punctate, pygidium covered by short, abundant golden setae, metasoma 1.05× length of mesosoma.

Male

Similar to female except differences described here: head bears black area between compound eyes; propodeum and first metasomal segment brown-yellow; hind tibiae without serration with short spines; tarsal claws bifid; body size slightly smaller.

Table 5. Diagnosis (modified from Turner, 1910).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by
Female	ANIC32_099267	24 May. 1972	QLD	18.1311S	139.5244E	G. B & S. R. Monteith
Female	ANIC32_099273	25 Oct. 1975	NT	16.47S	135.45E	J. C. Cardale
Male	ANIC99272	3 Oct. 1950	QLD	19.568516S	147.406387E	E. F. Riek

Remarks

Original description of this species by Turner, 1910 was based on one sex only (female).

Distribution: QLD. New records: NT.

Heterodontonyx prapositus (Haupt, 1935).

Cryptochilus (*Cryptochilus*) *praepositus* Haupt, 1935b: 269. Type data: holotype HUM, Type locality: WA, SA, Tas., Celebes. Elliot, 2007: 21 [cat.].

Material examined

Holotype images

Holotype is female and from a Bingham collection. From the label, it seems that Haupt determined the specimen in 1920s, but formally described the species in 1935. Male specimen was also first studied and labelled by Haupt in 1920s and later in 1995 the "allotype" was designated as lectotype by Raymond Wahis. Both specimens are kept in HUM and are in good condition.

Other material (See Table 6):

Length 10 - 25 mm; colour black and orange; body moderately setose; head of female with face and vertex yellow orange, except for a black band as wide as ocellar triangle passing through ocelli and reaching compound eyes; head of male with vertex and disc of frons black; propodeum without tubercles; second metasomal segment sometimes with a very narrow, apical black band in male, sometimes without it in female.

Redescription

Female

Coloration. Head orange yellow except for a narrow area between the eyes, and the end of the mandible, which are dark/black; mesosoma black except for tegula which is orange; tibiae and tarsi orange, femora black basally, orange apically;

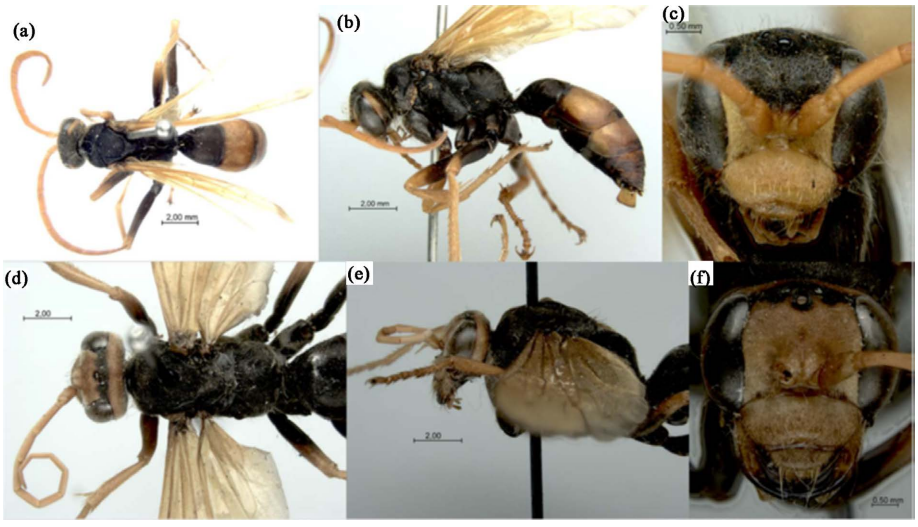

Figure 9. (a)-(c) *Cryptochilus praepositus* male lectotype (a) Dorsal view (b) Lateral view, left side (c) Head, frontal view (d) (f) *Cryptochilus praepositus* female holotype (d) Dorsal view (e) Lateral view, left side (f) Head, frontal view. Scale bars (a), (b), (d), (e): 2 mm, (c), (f): 5 mm. Images taken by Lars Krogmann from HUM.

Table 6. Diagnosis (modified from Haupt, 1935).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by
Female	ANIC 32_101102	21 Oct. 1949	NSW	32.03S	147.98E	Paramonov, S. J.
Female	ANIC 32_099228	Oct. 1972	QLD	24.87S	152.35E	H. Frauca
Female	ANIC32_099287	2 Jan. 1987	NSW	35.15S	149.96E	Naumann, I. D.
Male	ANIC32_101057	23-27 Sept. 1969	WA	26.65S	120.25E	H. Evans, R. W. Matthews
Male	ANIC32_099249	24 May. 1972	QLD	17.9S	139.6E	Monteith, G. B. & Monteith, S. R.
Male	ANIC32099245	27-28.Sept. 1972	NT	25.3S	135.5E	Z, Liepa
Male	WAM. E101033	1 Apr. 1980	SA	31.82S	138.59E	Bohart, R. M.
Male	ANIC32_100972	29 Nov. - 2 Dec. 1981	NSW	31.05S	141.42E	Cardale, J. C.
Male	ANIC32_100975	29 Nov. - 2 Dec. 1981	NSW	31.05S	141.42E	I. D. Naumann, Cardale, J. C.
Male	ANIC32_101028	12 Nov. 1987	SA	34.01S	139.49E	Naumann, I. & Cardale, J

first metasomal segment black, second metasomal segment orange, sometimes with narrow apical black band, remainder yellow orange; wings yellow orange, with a narrow apical darkening.

Head. Head wider than long, TFD/FD = 1.21; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.66; frons with median line not reaching median ocellus; apical margin of clypeus straight; clypeus medium, clypeus length: width = 2.08; labrum on same plain as clypeus completely exposed beneath; malar space very short, almost non-existent; first flagellarsegment about the same length as the second.

Mesosoma. Mesosoma covered with blacksetae, pronotum relatively short, with a very weak median line, its posterior margin angulate; metanotum knobbed; metapostnotum suppressed; propodeum wrinkled across with noobvious median line, without tubercules; dorsal edge of hind tibia with spine-bearing scalelike elevations which becomes less prominent towards tarsus; tarsal claws dentate.

Metasoma. Metasoma with black setae, sparsely punctate, pygidium covered by short, abundant setae, metasoma 1.17× length of mesosoma.

Male

Similar to female except differences described here: vertex and frons black; clypeus convex, apical margin straight, labrum completely exposed beneath; hind tibiae without serration with short spines; body size slightly smaller.

Distribution: SA, Tas., WA, Sulawesi (Celebes).

New records: NSW, Qld., NT.

Heterodontonyx solomonis Turner

Type data: Holotype whereabouts unknown; probable type depository Natural History Museum of Denmark Banks, 1941: 233.

Material examined

One non-type female specimen studied from Solomon Islands; Accession number BM-048, collected by R.A. Lever and determined by R. Wahis in 1967.

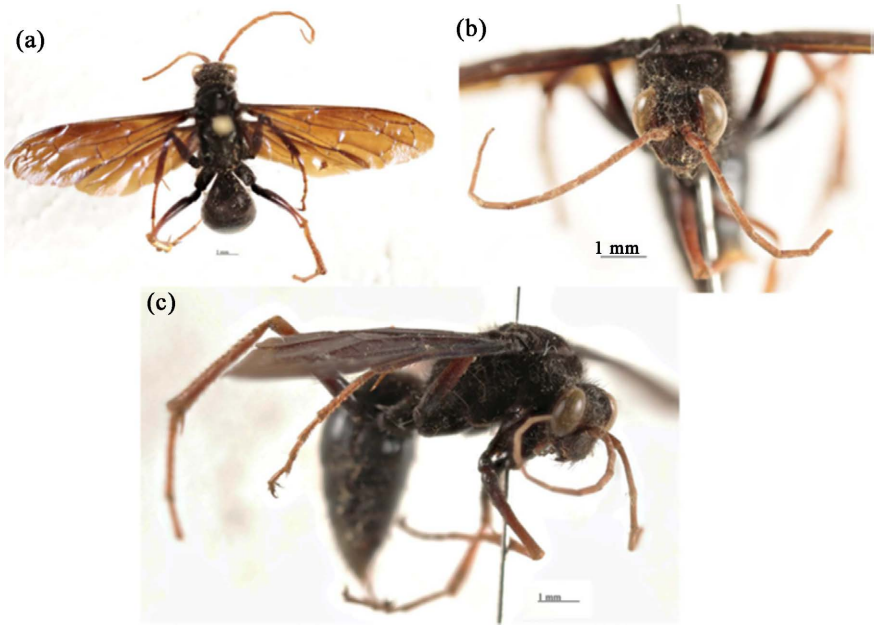

Figure 10. (a)-(c) *Heterodontonyx solomonis* female non-type (a) Dorsal view (b) Head, frontal view (c) Fronto-lateral view, right side. Scale bars: 1 mm.

Diagnosis (modified from Banks, 1941)

Length 35 mm; colour black; body heavily covered with black setae; head of female black; mesosoma black except for brown wings and legs; propodeum with half-tubercles; metasomal segments black.

Redescription

Female

Coloration. Head black except for antenna which is dark brown; mesosoma black; tibiae and tarsi brown; femora black basally, brown apically; metasomal segments black; wings dark brown.

Head. Head wider than long, TFD/FD = 1.2; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.88; frons with median line not reaching median ocellus; clypeus rather short, clypeus length: width = 2.6; labrum on same plain as clypeus, slightly exposed beneath; malar space very short, almost non-existent; first flagellar segment longer than the second.

Mesosoma. Mesosoma setose; pronotum relatively short, with weak median line, its posterior margin angulate; metanotum without knob; propodeum wrinkled across with a median line; without any prominent tubrcles (half-tuberculate); dorsal edge of hind tibia with spine-bearing scale-like elevations; tarsal claws dentate.

Metasoma. Metasoma setose, densely punctate, pygidium covered by short, abundant black setae, metasoma 1.13x length of mesosoma.

Male: Unknown

Distribution: Guadalcanar Island, Solomons

Heterodontonyx tuberculatus (Smith, 1855)

Pompilus tuberculatus Smith, 1855: 166. Type data: type BMNH, female. Type

locality: Western Australia (as New Holland (Houtman's Abrolhos, W. Coast)); Froggatt, 1892: 214 [cat.]. *Priocnemis tuberculatus* (Smith, 1855) comb. nov. Eliot, 2007: 30 [cat.] *Cryptochilus* (*Prionocnemis*) *tuberculatus* Schulz, 1908:471 [comb. nov., descr., dist.]. *Salius Tuberculatus* Tillyard, 1926: 292 [note].

Material examined

Holotype

Holotype is female and kept in BMNH with accession number: 185510577164. The specimen is in fair condition; antennae tips and right hind tarsus broken.

Other material (See Table 7):

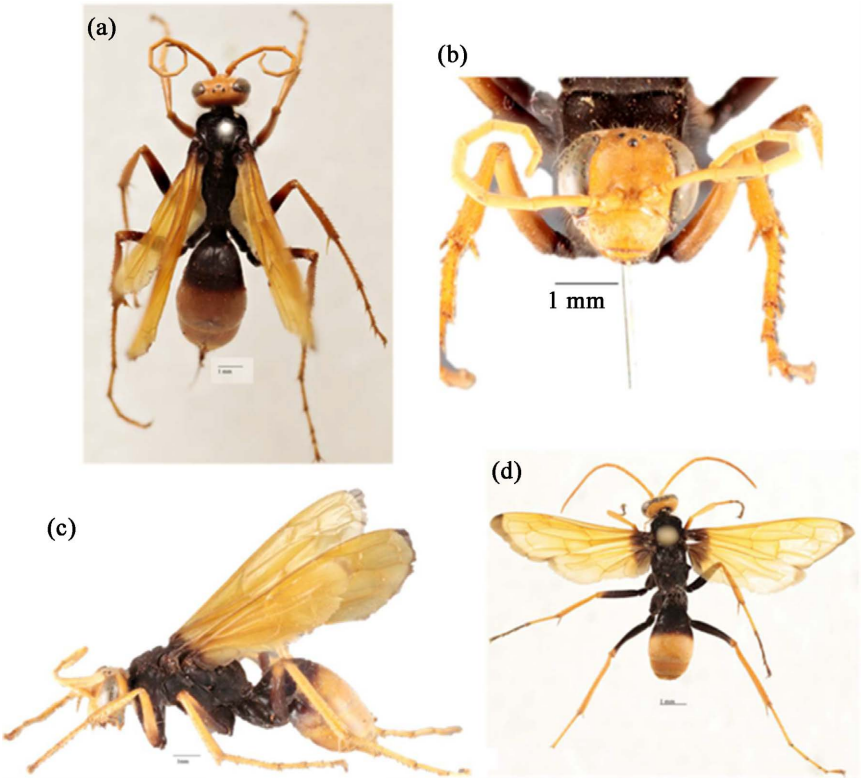

Figure 11. (a)-(c) *Heterodontonyx tuberculatus* female non-type (a) Dorsal view (b) Head, frontal view (c) Lateral view, left side (d) Male, non-type, dorsal view. Scale bars: 1 mm.

Table 7. Diagnosis (modified from Smith, 1855).

Gender	Accession #	Collection date	Locality	Latitude	Longitude	Collected by
Female	ANIC32_096531	12 Nov. 1953	WA	20.5167S	115.5333E	T. G. Capbell
Female	ANIC32_096627	20 Dec. 1984	NSW	34.51S	150.44E	D. B. McCorquodale
Female	ANIC	20 Mar. 1990	Qld.	27.56S	145.47E	E. D. Edwards, J. H. Fisk
Female	AM K551011	12 Apr. 2007	Qld.	14.40S	145.28E	R. B. Lachlan
Female	ANIC specimen	19 Mar. 2016	SA	27.44.99S	138.14.42E	D. K. Yeates, Y. N. Su & A. Lanford
Female	ANIC	21 Mar. 2017	NT	19.4914S	132.5510E	Unknown
Male	AM K513656	May. 1927	PNG	8.9353S	148.1664E	C. T. McNamara

Length 20 - 40 mm; colour black and orange; body heavily covered with setae, head of female entirely orange, head of male orange except for a black band as wide as ocellar triangle passing through ocelli and reaching compound eyes; propodeum with two distinct tubercles; second metasomal segment orange, without apical black band.

Redescription

Female

Coloration. Head orange yellow except for the end of the mandible which is dark; mesosoma black; tibiae and tarsi orange, femora black basally, orange apically; first metasomal segment black, second metasomal segment onward orange; wings yellow orange, with a narrow apical darkening.

Head. Head wider than long, TFD/FD = 1.18; posterior ocelli closer to each other than to the compound eye, POL: OOL = 0.68; frons with median line reaching median ocellus; apical margin of clypeus straight; clypeus medium, clypeus length: width = 2; labrum on same plain as clypeus slightly exposed beneath; malar space very short, almost non-existent; first flagellar segment clearly longer than the second.

Mesosoma. Setose; pronotum relatively short, with a median line, its posterior margin angulate; metanotum knobbed; metapostnotum suppressed; propodeum wrinkled across with amedian line, tuberculate; dorsal edge of hind tibia with spine-bearing serration; tarsal claws dentate.

Metasoma. Metasoma with less setae than mesosoma, softly punctate, pygidium covered by short, golden setae, metasoma 1.15× length of mesosoma.

Male

Similar to female except differences described here: inter-ocellar line containing ocelli black; clypeus slightly longer with labrum more exposed beneath; first flagellar segment slightly longer than the second; hind tibiae without serration with short spines; tarsal claws bifid; body size smaller.

Distribution WA.

New records: Qld., NT, SA, NSW, PNG.

Heterodontonyx wahisi Chavoshi sp. Nov.

Holotype

Holotype male from Australia: New South Wales: 5 km North Pooncarie; 27.11.1988.

N.W.Rodd; (AM-K551514)

Paratypes

Two male paratypes from SA and Qld.

Holotype and paratypes deposited in ANIC.

Diagnosis

Length 30 - 35 mm; colour black and orange; body heavily covered with black and golden setae; head of male with face and vertex yellow orange, except for a black band as wide as ocellar triangle passing through ocelli and reaching compound eyes; pronotum orange; propodeum with two distinct tubercles; second metasomal segment with apical black band.

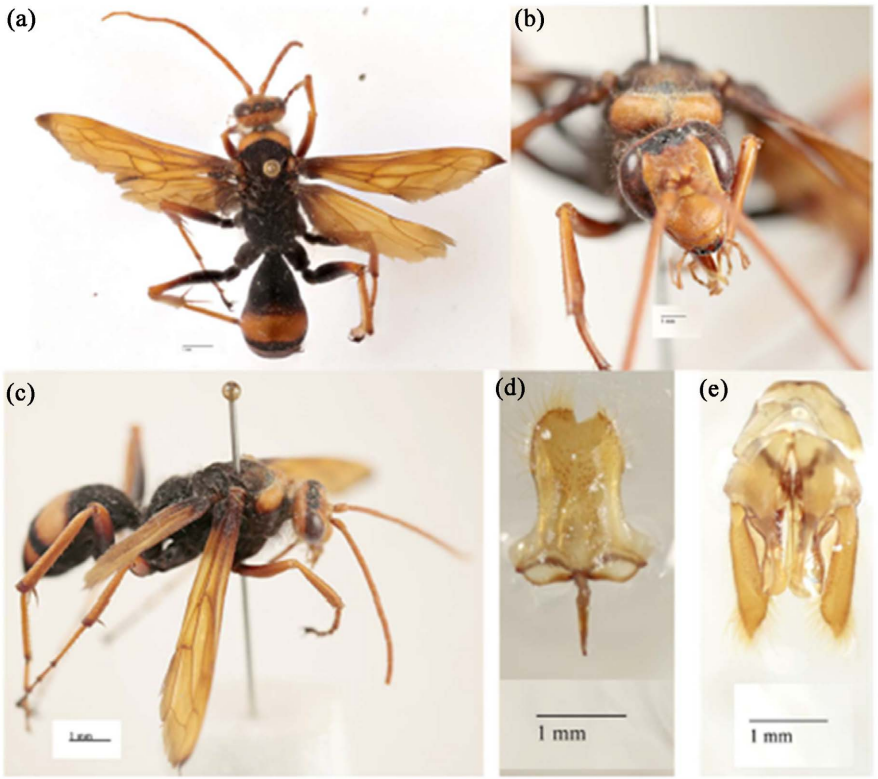

Figure 12. (a)-(e) *Heterodontonyx wahisi* male holotype, (a) Dorsal view (b) Head, frontal view (c) Lateral view, right side (d) Subgenital plate (e) Genitalia, scale bars: 1 mm.

Description

Male

Primarily based on holotype

Coloration. Head orange yellow except for a narrow area between the eyes and the end of the mandible, which are dark/black; mesosoma black except for tegula and pronotum which are orange; tibiae and tarsi orange, femora black basally, orange at apex; first metasomal segment black, second metasomal segment orange with apical black band, remainder yellow orange; wings yellow orange, with apical and basal darkening.

Head. Head almost the same width as length, TFD/FD = 1.02; posterior ocelli as far apart from each other as from the compound eye, POL: OOL = 1; eyes slightly convergent toward the vertex; frons with median line reaching median ocellus; apical margin of clypeus slightly convex; clypeus ratherlong, clypeus length: width = 1.42; labrum on same plain as clypeus moderately exposedbeneath; malar space very short, almost non-existent; antenna long but not very slender; firstflagellar segment longer than the second.

Mesosoma. Setose; pronotum relatively short, with an obvious median line, its posterior margin angulate; metanotum knobbed; metapostnotum suppressed; propodeum weakly wrinkled across with no obvious median line, tuberculate; dorsal edge of hind tibia with spine-bearing scale-like elevations which becomes lessprominent towards tarsus; tarsal claws dentate.

Metasoma. Metasoma polished, sparselypunctate, pygidium covered by short, abundant golden setae, metasoma almost the samelength of mesosoma.

Genitalia. Parapenial lobe elongate and slender, broad, 0.75× as long as entire genitalia; length 0.63× paramere length; setae long, thin abundant on external surface. Aedeagus almost the same length as parapenial lobes. Paramere length 0.83× total genitalia length; apex rounded; setaelong, thick, covering 0.3 of length apically. Sub genital plate, wide, apex rounded, setae abundant apically, long, thin.

Etymology

This species is named after late Raymond Wahis, who, along with his long-standing work on Pompilidae taxonomy, has contributed to knowledge of Australian *Heterodontonyx* Distribution.

4. Discussion

This study was the first ever updated species-level taxonomy for the Australasian *Heterodontonyx*. Molecular clues and traditional morphological characters were useful in delimiting one new species from *Heterodontonyx* stored in museum collections. We present phylogeny, molecular species delimitation and systematic revision of the genus *Heterodontonyx* including diagnosis and description for 10 species. New geographic records are shown for seven species and undescribed sexes are described for the first time from identified material for four species: *H. bicolor*, *H. distinctus*, *H. fulvidorsalis* and *H. tuberculatus*. A new host-association is made for *H. bicolor*: *Isopedellaleai* (Hirst) based on the identification of the host by spider species author (Hirst). Due to difficult access to the type of material of *H. tuberculatus* (deposited in BMNH) we have used images of non-type material (**Figure 11**). We were also unable to find type depositories of two species: *H. erythroura* and *H. solomonis* and as such we imaged two non-type specimens and used their original description as well as geographic data as a means of identification verification. These two species were not catalogued in Elliot, 2007 since their distribution is outside Australia (PNG and Solomon Islands).

5. Conclusion

This study reports the first molecular phylogeny of *Heterodontonyx* and provides new insights into the evolution of diversity in this pompilid group using assemblies of whole-genome data of pinned museum specimens. Molecular species delimitation complemented with morphological examination recovers one new species, three new sex associations and seven new records.

Acknowledgements

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Conflicts of Interest

The authors declare no conflicts of interest regarding the publication of this paper.

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