

# Molecular phylogeny of Ateleutinae (Hymenoptera: Ichneumonidae): systematics and biogeography of a widespread parasitoid wasp lineage

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Received 20 March 2018; revised 25 June 2018; accepted for publication 6 September 2018

The phylogeny of the ichneumonid parasitoid wasp subfamily Ateleutinae is investigated based on molecular data from five genes. A total of 36 species are included in the ingroup. Maximum likelihood analyses recovered a strongly supported monophyletic clade circumscribing the subfamily Ateleutinae. Five main clades were recovered in the subfamily, but relationships between these clades were mostly poorly supported. A new genus is identified and described: *Duvalia Santos gen. nov.* from Australia, which corresponds to the earliest known diverging lineage of Ateleutinae. *Duvalia perula Santos sp. nov.* is described and illustrated. The genus *Ateleute* is shown to be paraphyletic with respect to *Tamaulipeca*, but further studies with more intense sampling of the Neotropical fauna are needed in order to provide a comprehensive classification of the genera within this subfamily. *Ateleute boitata Santos sp. nov.*, a morphologically aberrant species from South America, is described to highlight the morphological diversity in the genus. All Old World species of *Ateleute* are recovered in a single clade. *Ateleute grossa* is newly recorded as a parasitoid of *Oiketicus kirbyi* (Lepidoptera: Psychidae). Diagnoses and identification keys to the genera of Ateleutinae are provided.

ADDITIONAL KEYWORDS: Cryptinae – Psychidae – bagworm – parasite – *Duvalia* – *Ateleute* – *Tamaulipeca*.

## INTRODUCTION

Ateleutinae are a small lineage of ichneumonid wasps currently including two genera and 46 species distributed almost worldwide (Bordera & Sääksjärvi, 2012; Yu *et al.*, 2012; Sheng *et al.*, 2013). The group was originally proposed as a subtribe of Cryptini (Cryptinae) based on a single genus, *Ateleute* Förster (Townes, 1967, 1970). Most species of *Ateleute* are from tropical and subtropical parts of the Old World, but the genus is also found in temperate zones in North America, Europe and Japan. There are no described species

from the Australasian region, but Gauld (1984) stated that several undescribed species were present in Australia. Ateleutinae were notably not recorded from the Neotropical region until Kasparyan & Hernandez (2001) described two species of *Ateleute* and a new genus, *Tamaulipeca* Kasparyan, from Mexico and Costa Rica. Bordera & Sääksjärvi (2012), studying the fauna from Western Amazonia, described five new species of *Ateleute* and three species of *Tamaulipeca*.

Ateleutinae have been regarded by many authors as anomalous and difficult to place within Ichneumonidae. Townes *et al.* (1961) had placed *Ateleute* in Phygadeuontini, but later (1967) considered it 'an isolated genus' of Cryptini (= Mesostenini of Townes), noting that it could actually be more related to the *Chirotica* Förster genus-group in Phygadeuontini, but

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[Version of Record, published online 30 November 2018; <http://zoobank.org/urn:lsid:zoobank.org:pub:74560B35-50C9-434F-A60A-32A6DF2928F9>]

preferred to place it within its own subtribe. Likewise, Gauld (1984) considered *Ateleute* a genus of unclear taxonomic placement, and Bordera & Sääksjärvi (2012) considered the tribe Ateleutina as ‘atypical Cryptini’. In the first phylogenetic analyses to include a sizable assemblage of Cryptinae, using data from 28S rRNA, the Ateleutina were recovered outside the Cryptini clade (Laurenne *et al.*, 2006; Quicke *et al.*, 2009). Their exact placement, however, varied depending on gap cost parameters. Under one gap cost regime, *Ateleute* was recovered as sister to Ichneumoninae, while in others it was sister to the phygadeuontine *Austriteles* Gauld (Laurenne *et al.*, 2006). With the addition of more taxa to the analysis, that clade also included *Tamaulipeca* and the phygadeuontine *Handaioia* Seyrig (Quicke *et al.*, 2009). The clade with Ateleutina and its closely related groups was sometimes recovered as sister to all other Cryptinae, sometimes as sister to a clade including mostly taxa from Aptesini (then called Hemigastrini). With such conflicting results, caused at least in part by problems with indels in the 28S sequences, the authors recommended that Ateleutina (and other groups) were treated as *incertae sedis* within Cryptinae (Laurenne *et al.*, 2006).

More recent and extensive phylogenetic analyses (Santos, 2017) showed more conclusively that *Ateleute* and *Tamaulipeca* are only distantly related to Cryptini, leading to the elevation of Ateleutina to subfamily status (Ateleutinae *sensu* Santos). Their exact sister group, however, varied according to optimality criteria, and a more thorough taxonomic sampling of Ichneumoniformes is clearly needed to resolve the phylogeny of the group. Although the evolutionary relationships of Ateleutinae are still not fully resolved, it is clearly a monophyletic group supported by both molecular and morphological evidence (Santos, 2017). Species of Ateleutinae seem to be parasitoids of larvae and pupae of bagworm moths (Lepidoptera: Psychidae), but host records are scarce (see Biology section for *Ateleute*, below).

Considering the morphological distinctiveness and worldwide distribution of Ateleutinae, knowledge of their biodiversity and internal classification is still scarce. This work aims to provide a first step in that direction. Herein we investigate the phylogeny of Ateleutinae, discuss the validity and relationships of the constituent genera of the subfamily and propose a new genus therein.

## MATERIAL AND METHODS

### TAXON SAMPLING

Representative specimens of 36 species of Ateleutinae were sampled for this study: 32 species identified as *Ateleute*, three species of *Tamaulipeca sensu* Kasparyan & Hernandez (2001) and a species representing a

putative new genus (Table 1). The outgroup consisted of 27 species from the ‘Ichneumoniformes’ clade of ichneumonids, including taxa from six subfamilies (Adelognathinae, Agriotypinae, Cryptinae, Ichneumoninae, Phygadeuontinae and Microleptinae). The choice of terminal taxa for the outgroup aims to represent a comprehensive sampling of the main lineages of Ichneumoniformes based on the results from previous analyses (Santos, 2017). The tree was rooted with *Agriotypus armatus* Curtis, since the Agriotypinae seem to be the earliest diverging lineage in Ichneumoniformes (Santos, 2017).

Species identification for *Ateleute* was complicated since there is no single comprehensive taxonomic treatment for the genus, while many species remain undescribed. Specimens examined for this work were compared to photographs of primary types of 27 species [all 23 species described by Seyrig, plus *A. carolina* Townes, *A. pallidipes* Ashmead, *A. rectinervis* (Morley) and *A. spinipes* (Cameron)]; authoritatively determined species of *A. densistriata* (Uchida), *A. linearis* Förster and *A. minusculae* (Uchida); and to descriptions and illustrations of the remaining species. Only eight of the 36 species examined fit previously described species, with the remaining 23 taxa corresponding to new species. Because a complete taxonomic revision of *Ateleute* is beyond the scope of the present work, and most new taxa are represented by singletons, description of these was not considered in the present study.

Institutional acronyms for the depositories of specimens used in descriptive taxonomy are as follows (curators in parenthesis): FSCA, Florida State Collection of Arthropods, Gainesville, FL, USA (E. Talamas). MZSP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (C.R.F. Brandão). USNM, National Museum of Natural History, Washington, DC, USA (R. Kula). WINC, Waite Insect and Nematode Collection, Adelaide, Australia (J. Jennings).

### TAXONOMY

All morphological methods and conventions, including morphological terminology and biometric ratios, follow Santos & Aguiar (2013), except for the following: ‘second trochanter’ is referred to as trochantellus; the ‘posterior transverse carina of mesothoracic venter’ is referred to as ‘posterior transverse carina of mesosternum’; and the cell 1+Rs is called ‘areolet’ for simplicity. The first and subsequent tarsomeres are referred to as t1, t2, t3, etc., while first and subsequent metasomal tergites are referred to as T1, T2, T3, etc. Biometric ratios used in descriptions are as follows: MLW, mandible maximum length/maximum width; MWW, mandible minimum width/maximum width; CWH, clypeus maximum width/maximum height; CWW, clypeus maximum width/minimum width; MSM, malar space

**Table 1.** List of specimens used in the phylogenetic analyses, with a summary of the number of molecular loci sequenced for each taxon ('1' in sequence columns = sequence obtained). Complete specimen information available at Supporting Information, Appendix S1. CAR, Central African Republic. USA, United States of America

Subfamily	Taxon	16S	28S	COI	NAD	Wg	Country
Adelognathinae	<i>Adelognathus</i> sp.	1	1	1	1	1	Canada
Agriotypinae	<i>Agriotypus armatus</i>	1	1	1	1	1	Czech Republic
Ateleutinae	<i>Ateleute alborufa</i>	1	1	1	1	1	Madagascar
Ateleutinae	<i>Ateleute amarakaeri</i>		1			1	Guatemala
Ateleutinae	<i>Ateleute ashaninka</i>	1	1			1	Brazil
<b>Ateleutinae</b>	<b><i>Ateleute boitata</i> sp. nov.</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>Brazil</b>
Ateleutinae	<i>Ateleute crocalis</i>		1	1	1		Madagascar
Ateleutinae	<i>Ateleute densistriata</i>		1	1	1		China
Ateleutinae	<i>Ateleute linearis</i>	1	1	1	1		Sweden
Ateleutinae	<i>Ateleute linearis</i>	1	1	1	1	1	Germany
Ateleutinae	<i>Ateleute nigriceps</i>	1	1	1	1	1	Madagascar
Ateleutinae	<i>Ateleute rectinervis</i>	1	1	1	1	1	South Africa
Ateleutinae	<i>Ateleute</i> sp. nov. 1	1	1	1	1	1	Kenya
Ateleutinae	<i>Ateleute</i> sp. nov. 2	1	1	1	1	1	Thailand
Ateleutinae	<i>Ateleute</i> sp. nov. 3	1	1	1	1	1	Australia
Ateleutinae	<i>Ateleute</i> sp. nov. 4	1	1	1	1	1	Malaysia
Ateleutinae	<i>Ateleute</i> sp. nov. 5	1	1	1	1	1	Malaysia
Ateleutinae	<i>Ateleute</i> sp. nov. 6	1	1	1	1	1	Madagascar
Ateleutinae	<i>Ateleute</i> sp. nov. 7		1	1	1	1	Mozambique
Ateleutinae	<i>Ateleute</i> sp. nov. 8	1	1	1	1	1	Uganda
Ateleutinae	<i>Ateleute</i> sp. nov. 9		1	1	1	1	Uganda
Ateleutinae	<i>Ateleute</i> sp. nov. 10	1	1	1	1	1	Uganda
Ateleutinae	<i>Ateleute</i> sp. nov. 11	1	1	1	1	1	Uganda
Ateleutinae	<i>Ateleute</i> sp. nov. 12		1	1	1		CAR
Ateleutinae	<i>Ateleute</i> sp. nov. 13		1	1	1	1	CAR
Ateleutinae	<i>Ateleute</i> sp. nov. 14	1	1	1	1	1	Australia
Ateleutinae	<i>Ateleute</i> sp. nov. 15		1	1	1	1	Papua New Guinea
Ateleutinae	<i>Ateleute</i> sp. nov. 16		1	1	1	1	Papua New Guinea
Ateleutinae	<i>Ateleute</i> sp. nov. 17		1	1	1	1	Papua New Guinea
Ateleutinae	<i>Ateleute</i> sp. nov. 18			1	1		Mozambique
Ateleutinae	<i>Ateleute</i> sp. nov. 19	1	1	1	1	1	Madagascar
Ateleutinae	<i>Ateleute</i> sp. nov. 20	1	1	1			Peru
Ateleutinae	<i>Ateleute</i> sp. nov. 21	1	1	1	1		Peru
Ateleutinae	<i>Ateleute</i> sp. nov. 22		1			1	Ecuador
Ateleutinae	<i>Ateleute</i> sp. nov. 23					1	Peru
Ateleutinae	<i>Tamaulipeca</i> sp. nov. 1	1	1	1	1	1	French Guyana
Ateleutinae	<i>Tamaulipeca</i> sp. nov. 2	1		1	1	1	Peru
Ateleutinae	<i>Tamaulipeca</i> sp. nov. 3	1	1	1		1	Ecuador
<b>Ateleutinae</b>	<b><i>Duvalia perula</i>, gen. et sp. nov.</b>	<b>1</b>	<b>1</b>	<b>1</b>	<b>1</b>		<b>Australia</b>
Cryptinae	<i>Messatoporus discoidalis</i>	1	1	1	1	1	USA
Cryptinae	<i>Lanugo schlingeri</i>	1	1	1	1	1	USA
Cryptinae	<i>Trychosis exulans</i>	1	1	1	1	1	USA
Cryptinae	<i>Ischnus cinctipes</i>	1	1	1	1	1	USA
Cryptinae	<i>Lymeon orbis</i>	1	1	1	1	1	USA
Cryptinae	<i>Mesostenus thoracicus</i>	1	1	1	1	1	USA
Cryptinae	<i>Polycyrtus neglectus</i>	1	1	1		1	USA
Cryptinae	<i>Cubocephalus</i> sp.	1	1	1	1	1	USA
Cryptinae	<i>Cryptus albitarsis</i>	1	1	1	1	1	USA
Cryptinae	<i>Glodianus</i> sp.	1	1		1	1	Brazil
Cryptinae	<i>Sphecochaga vesparum</i>	1	1	1		1	USA
Cryptinae	<i>Thrybius togashii</i>	1	1	1	1	1	South Korea



**Table 2.** Primer sequences and PCR protocols used in this study

Marker	Primer name	Source	Sequence	Annealing, extension temperature (°C)
16S	16SAr	Palumbi (1996)	CGCCTGTTTATCAAAAACAT	47, 72
	16SBr	Palumbi (1996)	CCGGTCTGAACTCAGATCACGT	
28S	For28Vesp	Hines <i>et al.</i> (2007)	AGAGAGAGTTCAAGAGTACGTG	49, 68
	Rev28Vesp	Hines <i>et al.</i> (2007)	GGAACCAGCTACTAGATGG	
COI	LCO_1490	Folmer <i>et al.</i> (1994)	GGTCAACAAATCATAAAGATATTGG	47, 68
	HCO_2198	Folmer <i>et al.</i> (1994)	TAAACTTCAGGGTGACCAAAAAATCA	
	COI-5	Simon <i>et al.</i> (1994)	AATTGCAAATACTGCACCTATTGA	
ND1	ND1F	Klopfstein <i>et al.</i> (2011)	ACTAATTCAGATTCTCCTTCTG	45, 68
	ND1R	Klopfstein <i>et al.</i> (2011)	CAACCTTTTAGTGATGCTATTAA	
Wg	Wg587F	Ward & Downie (2005)	TGCACNGTGAARACYTGCTGGATG	54, 72
	WgAbR	Abouheif & Wray (2002)	ACYTCGCAGCACCARTGGAA	

**Table 3.** Summary of information for each locus of the molecular dataset, including average length of unaligned sequences; length of the aligned dataset; number of invariable, unique (autapomorphic) and parsimony informative sites; and GC content

	Unaligned	Aligned	Invariable	Unique	Pars. informative	GC
<b>16S</b>	496.8	635	343	65	227	20.1%
<b>28S</b>	763.5	876	646	99	131	58.1%
<i>COI</i>	652.5	728	383	59	286	27.3%
<i>ND1</i>	448.4	489	172	61	256	18.2%
<i>Wg</i>	427.4	464	304	26	134	55.4%

against published amino acid sequences in Genbank. Alignment of the two ribosomal loci was done using the E-INS-I algorithm, which is suitable for sequences with large unalignable regions. Since ribosomal sequences are notorious for alignment problems (e.g. Lutzoni *et al.*, 2000; Noé & Kucherov, 2004; see Laurene *et al.* 2006 specifically for ichneumonids), we explored the differences in the results obtained when using Gblocks v.0.91b (Castresana, 2000) to eliminate poorly aligned positions and divergent regions from the ribosomal loci. The program was implemented through its online server ([http://molevol.cmima.csic.es/castresana/Gblocks\\_server.html](http://molevol.cmima.csic.es/castresana/Gblocks_server.html)) using both the default configuration and the parameters to allow for a less stringent selection.

The most appropriate models and partitioning schemes were tested using PartitionFinder v.2.1.1 (Lanfear *et al.*, 2012), employing the 'greedy' search algorithm under the Bayesian Information Criterion (Table 4). Models that estimated a proportion of invariable sites ('+I' parameter) were not considered to avoid the risk of overparametrization (Mayrose *et al.*, 2005; Stamatakis, 2006). Phylogenetic analyses were conducted under maximum likelihood (ML) using GARLI 2.0 (Zwickl, 2006), with 50 independent search replicates with 50 attachment sites evaluated per

**Table 4.** Best-fit substitution models for each data subset indicated by PartitionFinder v.2.1.1 (Lanfear *et al.* 2012)

Subset	Best model
16S rRNA	GTR+G
28S rRNA	GTR+G
<i>COI</i> position 1	GTR+G
<i>COI</i> position 2	GTR+G
<i>COI</i> position 3	GTR+G
<i>ND1</i> position 1	GT+G
<i>ND1</i> position 2	HKY+G
<i>ND1</i> position 3	HKY+G
Wingless position 1	JC
Wingless position 2	SYM+G
Wingless position 3	HKY+G

taxon. Each search used four individuals per generation, holding over 1 per generation with a selection intensity of 0.5 and no penalty for holdover. Selection strength parameters establishing the relative weights of topology rearrangements, branch lengths and model parameter estimates were set to 0.01, 0.002 and 0.002, respectively. Each search replicate was set to run for 5 000 000 generations, or after running for 5000 generations without a change in tree topology.



Clade support was estimated by bootstrapping, running 100 replicates, searching on each replicate twice, and stopping each replicate after 2500 generations without a topological improvement. All other configuration values remained the same. Bootstrap values were plotted onto the maximum likelihood tree using the SumTrees command (sumtrees.py boot.tre – target = best.tre – output = mapped.tre) in the DendroPy python package (Sukumaran & Holder, 2010).

## RESULTS

The Maximum Likelihood tree (log likelihood = –37080.14709; Fig. 1) yielded a monophyletic Ateleutinae with very strong support (1.00 bootstrap). The clade was recovered as the sister group of Ichneumoninae, but with low support (0.23 bootstrap).

Within Ateleutinae, the earliest diverging lineage corresponds to a single Australian species that shows several unique morphological traits within the subfamily and is here treated as a new genus, *Duwalia* Santos gen. nov., characterized by having the clypeal margin laterally projected as triangular lobes; epicnemial carina ventrally distinct; T1 stout and posteriorly strongly expanded, its dorsolateral carina present; and ovipositor 0.34 × as long as hind tibia, its tip sagittate with ridges on the dorsal valve.

The remainder of the ateleutine tree comprises four main lineages: a grade of three Neotropical groups plus one single clade containing all of the Old World species of *Ateleute*. The latter comprises a highly supported (1.00 bootstrap) and morphologically consistent group, with at least four diagnostic characters observed in all examined specimens: (1) clypeal margin truncate or slightly convex, never medially invaginated (Fig. 2B); (2) fore wing cross-vein 3r-m present, even if unpigmented (Fig. 2C); (3) T1 with fine to distinct longitudinal striae (Fig. 2D); (4) propodeum without longitudinal carinae (Fig. 2D). The type species of the genus, the Palearctic *A. linearis* Förster, is part of this group.

The robustness of the Old World clade of *Ateleute* contrasts with the lack of consistency observed across the three Neotropical clades; while three consistent groups were recovered (bootstrap 0.75–1.00), the relationships among them are poorly supported (0.08–0.44 bootstrap) and varied according to model selection and the exclusion of different amounts of suboptimally aligned ribosomal partitions (Supporting Information, Appendix S2). One of these lineages includes the species of *Tamaulipeca*, a group readily diagnosed by the medially pointed apical margin of the clypeus (Fig. 6A) and the fore wing cross-vein 3r-m absent, and veins 3-Rs and 3-M distinctly divergent (Fig. 6B). The other

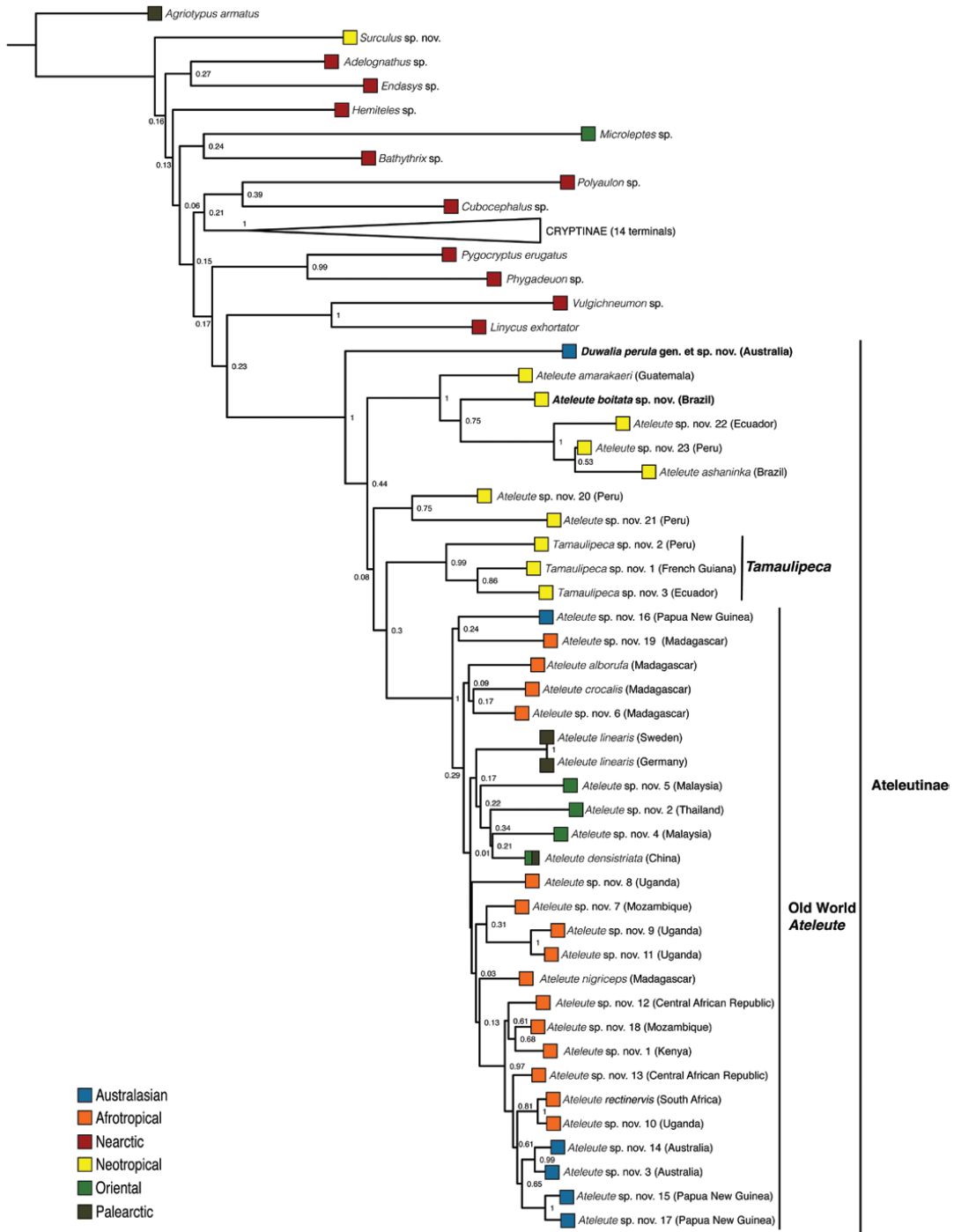
two Neotropical clades, however, are morphologically heterogeneous. Characters that are constant for *Tamaulipeca* and for the Old World *Ateleute* (which we suggest henceforth treating informally as *Ateleute* s.s.) are highly variable: clypeal margin broadly truncate to moderately emarginate (Fig. 3A); T1 with or without longitudinal striae; fore wing cross-vein 3r-m present or absent, veins 3-Rs and 3-M parallel to slightly divergent; and propodeum with or without longitudinal carinae.

This Neotropical assemblage includes at least one morphologically aberrant species, *A. boitata* Santos sp. nov. The new species appears to be closely related to *A. grossa* Kasparyan & Hernandez, for which DNA-grade specimens could not be obtained: both species are much larger than other *Ateleute* and show distinctive morphological features (see Taxonomy section). However, *A. boitata* sp. nov. was also recovered as closely related to ‘regular’ species of Neotropical *Ateleute*, complicating the establishment of a morphologically sound generic classification (see Discussion below).

## DISCUSSION

The topology recovered in the present analyses confirms the monophyly of Ateleutinae and reinforces the results of Santos (2017) in which the group was shown to be only distantly related to Cryptinae. In fact, the branch leading to Ateleutinae was the longest internal branch in the tree, corroborating the observations by previous authors (Townes, 1967; Gauld, 1984; Bordera & Sääksjärvi, 2012) about the morphological ‘uniqueness’ of *Ateleute*.

Whereas the status of Ateleutinae as a monophyletic and distinct subfamily is well supported and corroborated here, its evolutionary affinities are still somewhat unclear. In the present analyses they were recovered as the sister group to Ichneumoninae, a different result from that recovered by Santos (2017), which found the Ateleutinae nested in a clade with species of ‘Phygadeuontini’ and also *Adelognathus* (Adelognathinae). In the present analyses the taxonomic sampling of Ateleutinae was fairly comprehensive, whereas the sampling of Ichneumoninae was far more restricted, and hence the results obtained for the relationship between these two taxa should be treated with caution. The genera previously recovered as closely related to Ateleutinae, the phygadeuontines *Austriteles* and *Handaioia* (Laurenne et al., 2006; Quicke et al., 2009) could not be obtained for sequencing. Considering the polyphyletic nature of Phygadeuontini (Santos, 2017; and present results), it is plausible that these taxa are indeed closely related to Ateleutinae, and that new subfamilies may need



**Figure 1.** Maximum likelihood phylogeny of Ateleutinae. Numbers at each node correspond to bootstrap values. Biogeographic region for the examined specimens indicated by colour codes. Branch connecting the outgroup taxon *Agriotypus armatus* to the remaining taxa shortened for visualization purposes.

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**Figure 2.** Typical representatives of species of *Ateleute*. A, *A. sp. nov.* 3, head and mesosoma, lateral view. B, *A. sp. nov.* 8, clypeus and mandible. C, *A. shuar*, fore wing; photo from [Bordera & Sääksjärvi \(2012\)](#). D, *A. sp. nov.* 10, propodeum and metasomal T1. E, *A. sp. nov.* 14 ovipositor tip. F–G, ovipositor sheath. F, *A. sp. nov.* 3. G, *A. sp. nov.* 8.

to be erected to accommodate the substantial morphological and evolutionary diversity found across phygadeuontines.

#### PARAPHYLY OF *ATELEUTE*

As per its current taxonomic definition ([Townes, 1970](#); [Kasparyan & Hernandez, 2001](#); [Bordera &](#)

[Sääksjärvi, 2012](#)), the genus *Ateleute* is rendered paraphyletic by *Tamaulipeca*, a group that is morphologically well-characterized and readily diagnosable (see Taxonomy section below). While the clade including the Old World taxa is stable and well-supported, the relationships among the Neotropical forms currently assigned to *Ateleute* have low support, and clade composition does not correspond to





**Figure 3.** *Ateleute* spp. A, *A. sp. nov.* 20, clypeal margin. B–C, *A. amarakaeri*. B, male habitus. C, hind femur and tibia.

any putative morphological synapomorphies. While these taxa still fit the ‘broad’ definition of *Ateleute*, the morphological variation observed across the examined species is much higher than previously recognized. Several described New World species, including most of the ones described by [Bordera & Sääksjärvi \(2012\)](#) and the only described Nearctic species of the genus, *A. carolina* Townes, could not be obtained for sequencing, and their affinities remain uncertain. Hence, further work with better sampling of the New World taxa is needed in order to provide a more thorough morphological characterization of the group and establish sound generic limits.

One obvious solution would be to synonymize *Tamaulipeca* in order to render *Ateleute* monophyletic. However, lumping all of the considerable phenotypic diversity of the group under a single genus is more likely to complicate classification and taxonomic identification. At the same time, considering the limitations of the results observed herein, attempting to provide a full generic classification based on the data presently available is clearly premature. Hence, it seems more appropriate to progressively delimit monophyletic and morphologically diagnosable groups as more data accumulates. The proposal of *Duwalia* gen. nov. represents a step towards that direction, while the description of

the aberrant *A. boitata* sp. nov. intends to highlight the unexplored phenotypic diversity in the genus.

#### BIOGEOGRAPHY

Drawing biogeographic inferences for Ateleutinae from the recovered tree topology is not straightforward. The fact that the earliest diverging lineages are all from the Neotropical or Australian regions may suggest that the subfamily as a whole has a Gondwanan history. Within *Ateleute*, all examined species that currently occur in areas geologically belonging to Laurasia (*A. linearis*, *A. densistriata* Uchida and three undescribed species from South-East Asia) were recovered in a single clade nested within a Gondwanan background. Species from Madagascar, the Afrotropical region at large and the Australasian region appear scattered across several groups within the clade.

It is tempting to hypothesize that these patterns may have been driven by past vicariance events, such as the break-up between Africa and South America separating the Neotropical lineages from the Old World clade. However, the taxonomic sampling of the current analyses is far from complete; many of the known species are not represented in the phylogeny, and the Ateleutinae as a whole clearly include many undescribed species.

In addition to that, the lack of information regarding divergence times casts doubt on whether the observed diversification patterns may be chronologically consistent with putative vicariant events. A vicariance-driven scenario would suggest the Ateleutinae as an ancient lineage within Ichneumonidae, as the oldest fossils known for the family date from the Lower Cretaceous (Zhang & Rasnitsyn, 2003; Kopylov, 2010; Kopylov & Zhang, 2015).

Currently there are no known fossils for Ateleutinae, and the currently precarious understanding of the ichneumonid fossil record (Spasojevic *et al.*, 2018) requires rigorous study and re-evaluation of fossil taxa before any reliable molecular-clock-type analysis to infer divergence timing for the subfamily. It is noteworthy that there seems to be little 'geographic conservatism' in the evolution of Ateleutinae; species occurring in each region seem to be derived from multiple lineages. This is consistent with a scenario of very old divergence times, predating vicariant events such as continental splits, but it may also suggest a considerable amount of dispersal among closely related lineages. For example, multiple lineages seem to be present in Madagascar, which separated from the Indian peninsula 88 Mya, and from Africa 135 Mya (Briggs, 2003; Ali & Aitchison, 2008). This implies either that these lineages were already present in Madagascar by then, or that dispersal between island and continent has subsequently occurred multiple times.

## SYSTEMATICS

### ATELEUTINAE TOWNES, 1970

*Diagnosis* Ateleutinae can be distinguished from all other subfamilies of Ichneumonidae by the combination of the following characters. (1) Clypeus moderately convex, separated from face by groove.

(2) Occipital carina dorsally absent, ventrally joining hypostomal carina near or at base of mandible. (3) Epomia absent. (4) Epicnemial carina ventrally absent except in *Duwalia* gen. nov. (4) Posterior transverse carina of mesosternum complete. (5) Propodeum anteriorly elongate, its spiracle closer to midlength than to anterior margin of propodeum. (6) Cross-vein 2m-cu distinct, with a single bulla. (7) First metasomal tergite without glymma, often with longitudinal striae, spiracle near its midlength. (8) Thyridium small or absent; gastrocoeli absent.

*Comments* Sexual dimorphism in most Ateleutinae is stronger than observed for many Ichneumonidae, and it is usually difficult to associate males and females of the same species. Males are usually much smaller than the respective females and show a general reduction of diagnostic features, including colour patterns; as a result, male specimens across multiple species often have a similar, generalized morphology. Bordera & Sääksjärvi (2012) observed a significant variation in clasper shape across males of South American Ateleutinae, which may be the most reliable character to differentiate species based on male specimens. Other secondary sexual differences are as follows: antenna with significantly more flagellomeres, each flagellomere usually shorter and wider; white band of flagellum, when present, starting more apically and usually covering more articles; transverse furrow at base of propodeum slightly longer; T1 more slender and less triangular; T1LWW usually less than 2.0; spiracle more distinctly prominent; metasomal segments 2–7 more slender.

In the new genus *Duwalia*, sexual dimorphism is much less pronounced than in the remaining Ateleutinae, and more similar to the pattern observed in Cryptinae and Phygadeuontinae. Since *Duwalia* represents the earliest diverging lineage in Ateleutinae, the higher degree of dimorphism seen in other groups of the subfamily appears to be a derived state.

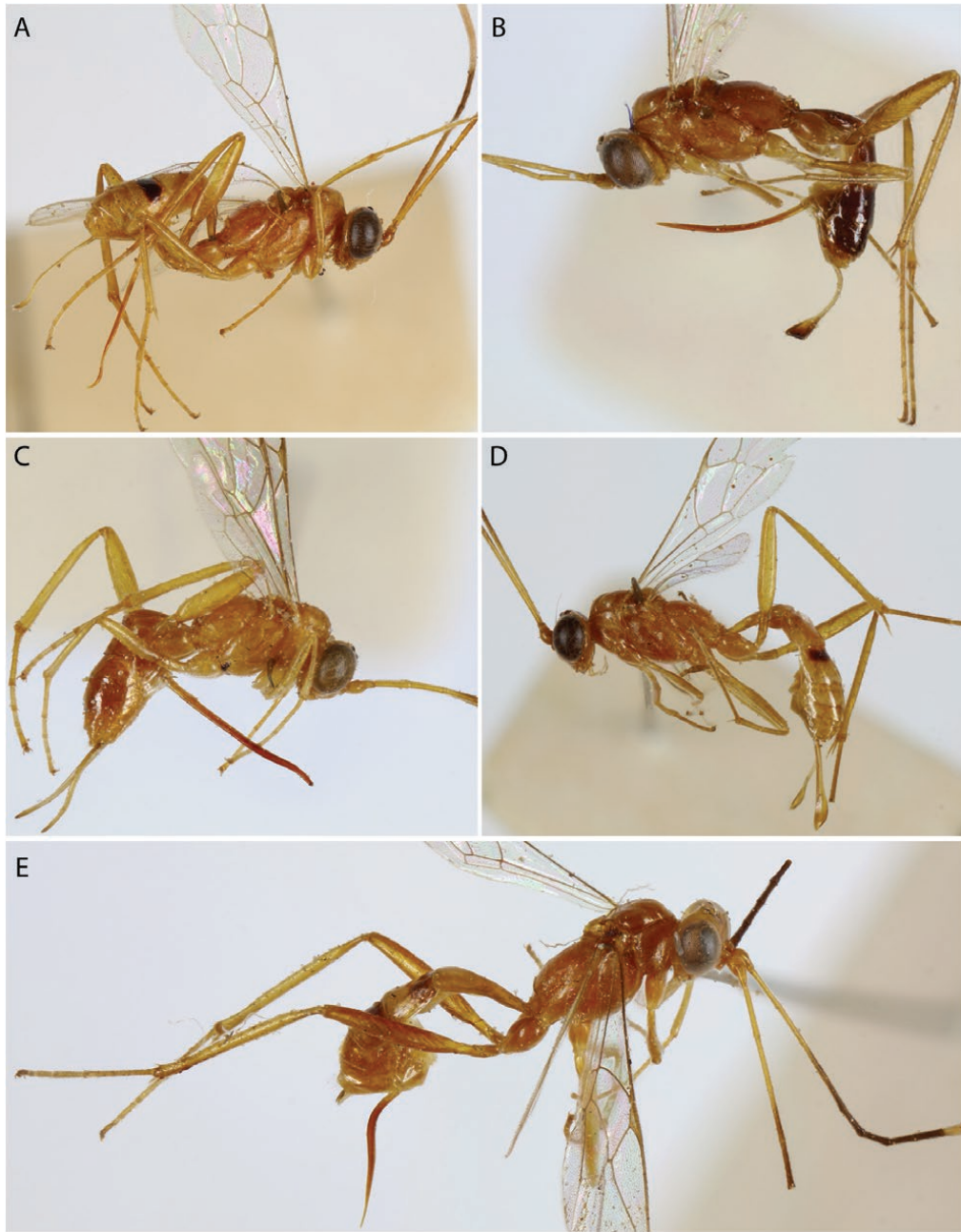
#### KEY TO THE GENERA OF ATELEUTINAE

1. Epicnemial carina ventrally distinct; ovipositor short, sheath  $0.35 \times$  as long as hind tibia, dorsal valve with distinct ridges (Fig. 7A, 7G); T1 stout, maximum width  $1.6 \times$  maximum length (Fig. 6F); hind wing vein 2-1A distinct, almost reaching wing margin; hind tibia of male with sparse small bristles (Fig. 7C). Australasian ..... *Duwalia* gen. nov.
- 1'. Epicnemial carina ventrally absent; ovipositor moderately long, sheath at least  $0.60 \times$  as long as hind tibia (Figs 4, 6D); dorsal valve without ridges (Figs 2E, 4A); T1 slender, maximum width  $>2.0 \times$  maximum length (Figs 2D, 5H, 6E); hind wing vein 2-1A almost always absent or vestigial; hind tibia of male densely covered with stout bristles (Fig. 3B–C) ..... 2
2. Clypeal margin truncate (Fig. 2B) to moderately convex (Fig. 3A); fore wing cross-vein 3r-m usually present, even if spectral, veins 3-Rs and 3-M parallel or almost so (Fig. 2C). Worldwide ..... *Ateleute* Förster
- 2'. Clypeal margin distinctly pointed medially (Fig. 6A); fore wing cross-vein 3r-m absent, veins 3-Rs and 3-M distinctly divergent (Fig. 6B). Neotropical ..... *Tamaulipeca* Kasparyan

Genera of Ateleutinae would run to Cryptinae in most published subfamily keys for Ichneumonidae (e.g. Wahl, 1993; Gauld, 2006; Wahl & Palacio, 2006); all examined taxa also run without problems to Ateleutina and *Ateleute* in the key by Townes (1970). The distinctive morphology of Ateleutinae when

compared to Cryptinae, as well as the diagnosis provided above, should suffice to allow recognition of the subfamily.

The new taxa proposed herein and the large number of putative new species of *Ateleute* in museum collections (e.g. several new species from the Oriental region



**Figure 4.** Holotypes of Madagascan *Ateleute* highlighting unusual ovipositor shapes. A, *A. crocalis*. B, *A. scalena*. C, *A. sinuata*. D, *A. foliacea*. E, *A. retorsa*.





**Figure 5.** Two unusually large-bodied species of *Ateleute*. A–C, E–F, H–J, *A. boitata* sp. nov. A, holotype habitus. B, paratype head in lateral view. C, holotype head in front view. E, holotype antenna. F, paratype propodeum. H, paratype metasomal T1. I, holotype ovipositor sheath. J, paratype ovipositor tip. D, G, *A. grossa*. D, habitus. G, propodeum.





**Figure 6.** *Tamaulipeca*. A–B, *T. bora*. A, clypeus and mandible. B, fore wing. C–E, *T. sp. nov.* 1. C, propodeum. D, metasoma and ovipositor. E, metasomal T1.

at BMNH; G. Broad, pers. comm.) suggest that the diversity of Ateleutinae is much higher than previously expected. The group has been poorly studied, maybe due to being considered part of an obscure lineage within Cryptini rather than as a distinct subfamily. The present taxonomic account is intended to serve as a first step towards a more comprehensive revision of the biodiversity of Ateleutinae.

#### ATELEUTE FÖRSTER, 1869

(FIGS 2–5)

*Ateleute* Förster, 1869: 171. Type species: *Ateleute linearis* Förster, included by Förster, 1871.

*Ateleuta* Schulz, 1906: 99. Emendation.

*Talorga* Cameron, 1911: 63. Type species: *Talorga sinipes* Cameron, by monotypy.

*Tsirirella* Seyrig, 1952: 45. Type species: *Tsiririella tsiriria* Seyrig, designated by Townes *et al.*, 1961.

*Psychostenus* Uchida, 1955: 32. Type species: *Psychostenus minusculae* Uchida, by original designation.

**Diagnosis** *Ateleute* can be distinguished from all other genera of Ateleutinae by the combination of the following characters. (1) Lateral carina of scutellum complete. (2) Anterior transverse carina of propodeum usually absent (Fig. 2D). (3) Median longitudinal carina almost always absent, in a few species faintly suggested. (4) Hind tibia of male densely covered with stout bristles. (5) Fore wing cross-vein 3r-m almost always present, even if spectral (Fig. 2C). (6) Veins 3-Rs and 3-M parallel or almost so. (7) Hind wing vein 2-1A absent or vestigial (except in *A. grossa* and *A. boitata* sp. nov.). (8) T1 slender, T1LW 2.0–2.4, its dorsal surface usually with longitudinal striae (Fig. 2D).

**Comments** As currently defined, *Ateleute* is a non-monophyletic and morphologically heterogeneous group including: (1) a well-supported and



**Figure 7.** *Duwalia perula* gen. et sp. nov. A, female habitus. B, clypeus and mandible. C, male habitus. D, propodeum. E, ovipositor sheath. F, metasomal T1. G, ovipositor tip.

well-characterized group of Old World species, defined by clear, diagnostic features (*Ateleute sensu stricto*); (2) a grade of Neotropical lineages that are

still poorly understood from a phylogenetic and morphological perspective. Some of the Neotropical taxa show traits that are not found among Old World



species, including the clypeal margin sublaterally emarginate (Fig. 3A; versus truncate, see Fig. 2B) and median longitudinal carina of propodeum distinct. At least two Neotropical species (*A. grossa* and *A. boitata* sp. nov.) are so morphologically divergent from other *Ateleute* (see below) that they would normally warrant separate generic status; and yet, based on the molecular analyses, *A. boitata* sp. nov. is closely related to *A. amarakaeri*, *A. ashaninka* and other 'regular-looking' species of *Ateleute*. Therefore, the tree topology does not support the establishment of a new genus to include this species and the morphologically similar *A. grossa*.

As a consequence, many of the characters that are diagnostic for the two other genera of Ateleutinae are variable within *Ateleute*. At the same time, most of its diagnostic features are shared with at least one other Ateleutine genus, and no unambiguous synapomorphy was identified for the genus. Furthermore, the difficulty of assigning the taxa used in the phylogenetic analyses to currently described species highlights the need for a comprehensive taxonomic assessment of *Ateleute*. Most of the species included in this work likely correspond to new species, although confirming this would require a more complete examination of the existing type specimens.

Important morphological variation in *Ateleute* s.s. includes: (1) the epicnemial carina, though ventrally absent in all species, is distinct on the mesopleuron in some species (completely absent in others); (2) anterior transverse carina of propodeum absent in most species to at least partially distinct; (3) male claspers with variable shape, from transversely truncate to narrow and pointed; (4) ovipositor sheath varying from pointed or rounded to narrowly truncate (Fig. 2F–G); (5) ovipositor shape very variable, at least in Madagascan taxa, including apically sinuous (Fig. 4A, C, E); decurved (Fig. 4B) or spatulate (Fig. 4D).

Species of *Ateleute* seem to be relatively rare in the Neotropical region. In South America, the extensive sampling reported in Aguiar & Santos (2010) did not yield even a single specimen, while Bordera & Sääksjärvi (2012) collected only 25 specimens, all from humid tropical forests. In Papua New Guinea and Madagascar, the genus seems to be proportionally more abundant, based on material examined from surveys in the two islands. Examination of tens of thousands of specimens of Ichneumonidae from several survey projects in other regions yielded only a few additional specimens. In fact, a sizable number of museum specimens are available from more extensively sampled regions (e.g. *Ateleute linearis* in the Palearctic region), but this may be due to cumulative, decades-long sampling effort rather than local relative abundance.

**Biology** The biology of *Ateleute* is poorly known, but it seems that its species are parasitoids of bagworms (Lepidoptera: Psychidae). Known records include *A. carolina* attacking *Astala confederata* (Grote & Robinson), reported by Townes (1967) and *A. minusculae* attacking *Eumeta minuscula* Butler (Uchida, 1955; Momoi, 1977; Nishida, 1983). The latter reference provides substantial information on the biology of *A. minusculae*, which seems to be a species-specific (or at least oligophagous) larval ectoparasitoid throughout the year. Females oviposit on larval instars 4 to 7 and the development of larvae and pupae takes between 18 and 22 days. The species was attacked by hyperparasitoids such as *Itopectis alternans* (Gravenhorst, 1829) (Ichneumonidae: Pimplinae). An unidentified species of *Ateleute* (possibly *A. boitata* sp. nov.) was reported attacking *Oiketicus kirbyi* (Guiling) in a technical agricultural report (Baronio *et al.*, 2012) in Brazil.

**Distribution** Almost worldwide. *Ateleute* is most common and species-rich in tropical and subtropical areas, particularly in the Old World. The Afrotropical region has the largest described species richness (24 species), but this account may be biased because of the detailed work of Seyrig (1952) on the Madagascan fauna. There are two species in the Eastern Palearctic from China and Japan, and *A. linearis* Förster occurs throughout most of Europe. Six species are recorded from the Oriental region (Malaysia, southern China and Okinawa). In the New World, three species are described from southern North America (*A. carolina* Townes, *A. grossa* and *A. tinctoria* Kasparyan & Hernandez) and six from South America (five in Bordera & Sääksjärvi, 2012, plus *A. boitata* sp. nov.). There are no described species for the Australasian region, but Gauld (1984) reports at least ten undescribed species from Australia, and at least five were examined in this study.

**Literature** Species descriptions and keys are available as follows: Nearctic (Townes, 1967; Kasparyan & Hernández, 2001); Neotropical (Kasparyan & Hernández, 2001; Bordera & Sääksjärvi, 2012); Afrotropical (Morley, 1917; Seyrig, 1952); Palearctic (Förster, 1871; Ashmead, 1906; Uchida, 1955); Oriental (Cameron, 1911; Uchida, 1955; Momoi, 1977; Sheng *et al.*, 2011, 2013).

#### ATELEUTE BOITATA SANTOS, SP. NOV.

(FIG. 5A–C, E, F, H–J)

**Diagnosis** *Ateleute boitata* can be distinguished from all species of *Ateleute* by the combination of the following characters. (1) Body relatively large (fore wing 8.9–10.0 mm long) and stout (Fig. 5A). (2) Head dorsoventrally elongate (1.8 × as tall as long in

lateral view; Fig. 5B). (3) Epicnemial carina completely absent. (4) Median longitudinal carina of propodeum distinct until posterior transverse carina (Fig. 5F). (5) Hind wing vein 2-1A distinct. Dorsal surface of T1 smooth (Fig. 5H). (6) Propodeum entirely ferruginous, with coarse wrinkles.

*Description of female holotype* Fore wing 8.9 mm long. Body shiny and mostly moderately pilose.

*Head:* Head in lateral view 1.8 × as tall as long (Fig. 5B). Mandible moderately short, MLW 1.3, its apex only slightly narrower than base, MWW 0.7; ventral tooth wide, trapezoidal, distinctly longer than dorsal tooth; malar space wide, MSM 1.0. Clypeus moderately convex, moderately wide, CHW 1.70, at midlength much wider than base, CWW 1.6, narrower again at apex; clypeal margin sharp, strongly lamellate, straight (Fig. 5C). Clypeus, supra-clypeal area and most of gena densely pilose; supra-antennal area, vertex and occiput glabrate. Supra-clypeal area rugulose-coriarius. Antenna with 36 flagellomeres; maximum width of flagellum about 1.7 × the minimum width of f1; flagellum subapically slightly enlarged, ventral surface flattened and rough around flagellomeres 9–30, strongly tapered towards apex (Fig. 5E). Supra-antennal area distinctly concave, longitudinally striate; ocellar area distinctly convex. Vertex and occiput slightly coriarius. Occipital carina ventrally joining hypostomal carina just before mandible base.

*Mesosoma:* Pronotum longitudinally striate, striae weak along posterior margin and strong over median transverse sulcus, dorsally with small coriarius-punctate area. Mesoscutum coriarius, shiny, with strong transverse wrinkles along notaulus. Scuto-scutellar groove distinctly striate. Lateral carina of scutellum complete. Mesopleuron anteriorly densely pilose, rugulose-reticulate, posteriorly sparsely pilose, coriarius. Subalar ridge narrow, keeled. Epicnemial carina entirely absent. Mesopleural fovea absent. Sternaulus complete but shallow throughout, carinulate, apical 0.5 almost indistinct. Propodeum 1.4 × as long as wide, covered by strong, widely spaced wrinkles. Anterior transverse carina of propodeum distinct, straight, fading out on median portion and after sublateral corner of propodeum (Fig. 5F). Posterior transverse carina complete, straight; area posteriorly to posterior carina with most wrinkles in longitudinal orientation. Median longitudinal carina distinct until posterior transverse carina; areola distinctly delimited, smoother than remainder of propodeum; lateral longitudinal carina vestigial, distinct only as short ridge. Tibiae and tarsi with sparse, moderately stout bristles. Fore wing vein 1-Rs+M sinuous, continuous with cross-vein 1m-cu, cross-vein 1m-cu

uniformly curved; cross-vein 1cu-a arising distad to base of 1M+Rs; vein 2Cua 1.5 × as long as cross-vein 2cu-a, veins angled at about 110°; APH 2.1; AWH 1.6; cross-vein 3r-m spectral; cross-vein 2r-m distinct but much shorter than 3r-m, veins parallel; vein 2-M about as long as 3-M. Hind wing vein 2-1A distinct, almost reaching wing margin; HW1C 2.3.

*Metasoma:* T1 smooth and polished T1LW 2.3, T1WW 3.5 (Fig. 5H). Spiracle placed on anterior 0.55. T2 approximately square, T2LW 0.9, T2WW 1.2; polished, slightly coriarius, laterally with short, sparse hairs. Thyridium very shallow, almost indistinct. Ovipositor sheath broadly truncate (Fig. 5I); ovipositor moderately long, OST 0.90, moderately stout, straight, its tip blunt, nodus absent, lower valve without distinct teeth (Fig. 5J).

*Colour:* Head black; basal 0.6 of mandible ferruginous, apical 0.4 reddish; f5–8, apex of f4 and base of f9, whitish. Mesosoma: ferruginous (197,104,003); dorsal 0.5 of pronotum, most of mesoscutum, axillary through and scutellum blackish; fore- and mid legs uniformly lighter from base towards apex, t1–4 pale yellow, t5 blackish; hind tibia and t1–4 abruptly light yellow, hind t5 brownish. Wings hyaline. Metasoma: T1 mostly ferruginous, posteriorly with blackish white spot covering 0.2 of dorsal surface, followed by narrow whitish (057,014,086) stripe. T2–7 blackish, posteriorly with broad whitish stripes, on T4–7 distinctly narrower on median portion; T8 black with whitish lateral marks. S2–5 mostly whitish with progressively smaller brownish or blackish spots; S6 entirely whitish. Ovipositor sheath blackish; ovipositor reddish.

*Male* Unknown.

*Variation* Fore wing 8.9–10.0 mm long. Antenna with 32–36 flagellomeres. Specimens from Brazil and Bolivia with mesoscutum entirely black, pronotum dorsal 0.6–1.0 black, and more extensive blackish marks on dorsal margin of mesopleuron; cross-vein 3r-m indistinct.

*Comments* *Ateleute boitata* is very similar to *Ateleute grossa*, from which it can be differentiated by the generally ferruginous tone of the mesosoma (vs. pale yellow); propodeum entirely ferruginous (vs. with ovoid blackish marks on anterior portion); and with coarse wrinkles, after posterior transverse carina mostly longitudinally oriented (vs. finely reticulate). The new species appears to be restricted to the southern half of South America, while *A. grossa* occurs in Central America (Costa Rica) and North America (Mexico, Tamaulipas).

The two species are a morphologically aberrant group within *Ateleute*, characterized by having larger body size (fore wing 5.9–10.0 mm long, vs. 2.2–6.0 mm



in most other species, except *A. minusculae* Uchida, which may also reach circa 10 mm); stout mesosoma; head dorsoventrally elongate (1.55–1.85 × as tall as long in lateral view); hind wing vein 2-1A distinct; and ovipositor approximately 0.8–0.9× as long as hind tibia, its apex blunt (vs. ~0.65× in most species, apex usually lanceolate). The evolution of these distinct traits within New World Ateleutinae is still to be elucidated through comparative studies including phylogenetic analyses of a more extensive taxonomic assemblage.

**Etymology** The specific epithet is a reference to the ‘mboi tatá’, a character from the Tupi people mythology meaning ‘fiery serpent’, in reference to the paratype locality, *Serra da Serpentina* (‘Serpentine’s highlands’), and to the bright ferruginous (‘fiery’) colour of the mesosoma of this species.

**Material examined** 4 ♀♀. **Holotype** ♀: ARGENTINA: La Rioja, Santa Vera Cruz, 1700 m, 15.XII.2003, C. Porter & L. Stange, Malaise trap (FSCA). Condition of type: pinned, intact. **Paratypes**: 1 ♀: ARGENTINA, La Rioja, El Duraznillo, ca. Cantadero, degraded wet forest, Dec.2001, Malaise trap, P. Fidalgo. 1 ♀: BOLIVIA, Santa Cruz, 40 km NW Santa Cruz, Porterillo del Guendá, 400 m, 17 Dec 2004, G. Nearns (FSCA). 1 ♀: BRAZIL, Minas Gerais, Conceição do Mato Dentro, Serra da Serpentina, area 2, 19.02495°S, 43.39019°W, 17–27.IV.2011, Malaise, R. R. Silva & E. Z. Albuquerque (MZSP).

**Distribution** Bolivia, Brazil (MG) and Argentina.

*ATELEUTE GROSSA* KASPARYAN & HERNANDEZ, 2001  
(FIGS 5D, 5G)

*Ateleute grossa* Kasparyan & Hernandez, 2001: 229. Holotype ♀ from Mexico, not examined.

**Comments** *Ateleute grossa* is very similar to the new species *A. boitata*, which occurs in South America. The two species have several slight differences in colour patterns, biometric ratios (see below) and sculpturing; most distinctly, *A. grossa* can be differentiated from *A. boitata* sp. nov. by the generally pale yellow tone of the mesosoma (vs. ferruginous); propodeum with ovoid blackish marks on anterior portion (vs. entirely ferruginous); and propodeum finely reticulate (vs. with coarse wrinkles).

The holotype was the only specimen examined by Kasparyan & Hernandez (2001), and no additional specimens were recorded in later accounts of the Mexican fauna (e.g. Kasparyan & Ruíz-Cancino, 2005). Herein we newly record the species from Costa Rica. The following morphometric measurements, based on the specimens examined for this work ( $N = 8$  females), are original information that complements the original description: fore wing 5.7–9.5 mm long; MLW 1.5; MWW 0.7; MSM 1.0; APH 1.4–1.5; AWW 1.8–1.9;

H1WC 1.6–1.8; T1LW 2.2–2.4; T1WW 3.0–3.2; spiracle of T1 placed on anterior 0.4; T2LW 0.9; T2WW 1.3; OST 0.85. The original description recorded MSM 0.85 and OST 0.75 for the holotype, which may correspond to geographical variation between populations in Mexico and Costa Rica. Other than that, the examined specimens accurately match the holotype description.

**Biology** All the females examined for this work were reared from Psychidae; five of them are recorded as parasitoids of *Oiketicus kirbyi*, a common pest of several crops in South and Central America, including banana, cocoa, oil palm, avocado, citrus and eucalyptus (Rhainds & La Rosa, 2010).

**Material examined** 8 ♀♀. 1 ♀ from COSTA RICA, Palmar, 19 Aug 1959, J. O. Harrison, ‘from bag worm’ (USNM). 2 ♀♀, same data except 20 Oct 1959, C. S. Stephens, ‘Psychidae parasite’. 5 ♀♀, same data except 15 Jan 1960, ex. *Oiketicus kirbyi* (USNM).

**Distribution** Mexico and Costa Rica.

*TAMAULIPECA* KASPARYAN, 2001  
(FIG. 6)

*Tamaulipeca* Kasparyan, 2001 in Kasparyan & Hernandez, 2001: 231. Type species: *Tamaulipeca clypeator* Kasparyan & Hernandez, by original designation.

**Diagnosis** *Tamaulipeca* can be distinguished from all other genera of Ateleutinae by the combination of the following characters. (1) Clypeal margin distinctly pointed medially (Fig. 6A). (2) Mandible small and slender, MLW around 1.80, MWW 0.6–0.6. (3) Lateral carina of scutellum incomplete, reaching about 0.5 its length. (4) Median longitudinal carina of propodeum absent. (5) Hind tibia of male densely covered with stout bristles. (6) Cross-vein 2r-m short, almost indistinct. (7) Veins 3-Rs and 3-M distinctly divergent (Fig. 6B). (8) Hind wing vein 2-1A absent or vestigial.

**Comments** Species of *Tamaulipeca* are similar to the Neotropical *Ateleute*, from which they can be readily differentiated by the clypeal margin medially pointed (vs. truncate or emarginate medially in *Ateleute*) and veins 3-Rs and 3-M distinctly divergent (vs. parallel); species of *Tamaulipeca* also have no trace of the cross-vein 3r-m. *Tamaulipeca* also shows a broader, stouter T1 (see T1WW 2.7–3.0, versus T1LW 2.0–2.4 in *Ateleute*). The anterior transverse carina of the propodeum is absent in all described species of *Tamaulipeca*, but the species examined herein has a distinct, though weak, anterior carina (Fig. 6C).

**Biology** Unknown.

**Distribution** Neotropical. The five species of the genus are recorded from Mexico, Costa Rica, Ecuador

and Peru. The specimens included in the present analyses, from French Guyana, Peru and Ecuador, likely represent three new species, but since only a single specimen was available for each putative species, these potentially new taxa will be addressed elsewhere.

*DUWALIA* SANTOS, GEN. NOV.

(FIG. 7)

Type species: *Duwalia perula* sp. nov., by monotypy and present designation.

**Diagnosis** *Duwalia* gen. nov. can be distinguished from all other genera of Ateleutinae by the combination of the following characters. (1) Epicnemial carina ventrally distinct, laterally reaching about 0.7 of distance to subalar ridge. (2) Median longitudinal carina of propodeum present, though weak. (3) Hind tibia of male with sparse small bristles. (4) Hind wing vein 2-1A distinct, almost reaching wing margin. (5) Ovipositor short, OST 0.35, straight, its tip sagittate, dorsal valve with distinct teeth.

**Description** Body small (fore wing 4.6–5.1 mm long), moderately slender, mostly shiny (Fig. 7A).

**Head:** Somewhat globose, in lateral view 1.4 × as tall as long (Fig. 7A). Mandible relatively long, MLW 1.8, its apex distinctly narrower than base, MWW 0.6; ventral tooth slightly longer than dorsal one. Malar space moderately wide, MSM 0.8. Clypeus wide, CHW 1.8, wider at its midlength, CWW 1.8, slightly convex; clypeal margin truncate, medially straight, without teeth or tubercles, laterally slightly projected as small triangular lobe (Fig. 7B). Antenna with 26 flagellomeres, with distinct whitish band; flagellum subapically slightly enlarged, tapered towards apex; apical flagellomere pointed, without thickened or modified setae. Supra-antennal area without horns or tubercles. Gena ventrally as wide as at its midlength. Occipital and hypostomal carinae ventrally linear, not raised as flanges, meeting at mandible base.

**Thorax:** Dorsal margin of pronotum regular, not swollen; outline of collar not bordered by carina; median portion of pronotum distinctly concave, forming a transverse sulcus between pronotal collar and posterior margin. Mesoscutum strongly convex, subcircular, 1.0 × as long as wide, shiny; notaulus long, reaching 0.7 of mesoscutum length, convergent, deeply impressed, its surface weakly carinulate. Lateral carina of scutellum incomplete, reaching about 0.5 of its length. Epicnemial carina ventrally distinct, laterally reaching about 0.7 of distance to subalar ridge. Sternaulus sharp and distinct on anterior 0.5 of mesopleuron, its surface distinctly crenulate. Posterior

transverse carina of the mesosternum medially linear, not projected. Transverse furrow at base of propodeum 0.10 × as long as propodeum. Juxtacoxal carina indistinct. Pleural carina complete.

**Propodeum:** Long, 1.5 × as long as wide, shiny (Fig. 7D). Anterior margin medially concave, laterally without teeth-like projections. Spiracle round. Anterior transverse carina vestigial. Posterior transverse carina distinct, complete, straight, sublaterally not forming distinct crests. Median longitudinal carina of propodeum distinct but fading before reaching posterior transverse carina.

**Wings:** Hyaline. Ramellus absent; cross-vein 1cu-a distinctly apicad to 1M+R; vein 2Cua 1.8 × as long as cross-vein 2cu-a; cross-vein 2m-cu slightly inclivous, slightly sinuous, its bulla occupying 0.4 of its length, placed anteriorly, almost touching areolet; areolet medium sized, APH 1.1, wider than long, AWH 1.6; cross-vein 3r-m spectral, almost indistinct; cross-veins 2r-m and 3r-m slightly convergent, cross-vein 2r-m distinct but much shorter than 3r-m; vein 3-Rs subparallel to 3-M; vein 4-Rs slightly shorter than vein 4-M. Hind wing vein 1-M+Cu apically distinctly convex; veins Cua and 1M forming approximately right angle; vein Cua much longer than cross-vein cu-a, HW1C 1.8; veins 2-Rs and Cub distinct, reaching wing margin even if apically nebulous, apical 0.5 of Cub slightly concave; vein 2-1A distinct, almost reaching wing margin.

**Metasoma:** T1 moderately short, about 0.4 × as long as T2–8 combined, stout, T1LW 1.6, apex much wider than base, T1WW 3.3 (Fig. 7F), distinctly depressed, its ventrolateral outline somewhat angled, anteriorly without lateral tooth, dorsally without distinct longitudinal striae; dorsal outline of T1 slightly and uniformly curved; spiracle of T1 placed on anterior 0.4, not prominent; dorsolateral carina distinct until spiracle; median dorsal carina entirely absent; ventrolateral carina distinct. T2 short, T2LW 0.6, apex much wider than base, T2WW 1.4; thyridium indistinct. T7–8 about as long as T5–6. Ovipositor sheath broadly truncate, slightly wider at apex than at midlength (Fig. 7E). Ovipositor short, OST 0.35, moderately slender, straight, distinctly compressed; apex of ovipositor sagittate, with slight nodus; dorsal valve with notch-like teeth (Fig. 7G).

**Comments** *Duwalia* is unique among Ateleutinae in having a complete epicnemial carina. In the two other genera of the subfamily, the carina is absent or indistinct at least on the mesosternum. The ovipositor is also distinct from the condition present in all other ateleutine taxa by being short (OST 0.35), having a sagittate tip and distinct teeth on the dorsal valve.

Since *Duwalia* occurs in sympatry with *Ateleute* in Australia, the two genera could be mistaken for each other. *Duwalia* can be differentiated from Australasian species of *Ateleute* by having the clypeal margin laterally slightly emarginate as a small triangular lobe (vs. broadly truncate, straight); median longitudinal carina of propodeum distinct (vs. absent); male hind tibia with sparse small bristles (vs. with dense stout bristles); hind wing vein 2-1A distinct, almost reaching wing margin (vs. indistinct); and the T1 much stouter (T1LW 1.6) and more triangular (T1WW 3.3), in contrast with the slender T1 in almost all species of *Ateleute* (T1LW 2.0–2.4, T1WW 2.1–2.7, usually <2.4).

**Etymology** The genus name stems from the Australian aboriginal word ‘duwal’, meaning a short spear with two barbs, and also a name for a clan from the Dua moiety. The name is a reference to the short ovipositor of *D. perula*, with ridges on the dorsal valve. *Duwalia* is to be treated as a feminine noun.

**Biology** Unknown.

**Distribution** Australia.

*DUWALIA PERULA* SANTOS, SP. NOV.

(FIG. 7)

**Diagnosis** See diagnosis for *Duwalia* gen. nov.

**Description of female holotype** Fore wing 5.1 mm long. Body moderately slender and shiny.

**Head:** Mandible, clypeus and supra-clypeal area covered with moderately dense, long hairs; MLW 1.8, MWW 0.6; ventral tooth, as robust as dorsal one, its tip lanceolate; MSM 0.8. Clypeus sparsely punctate; CHW 1.8, CWW 1.8, apex narrower than midlength. Supra-clypeal area coriarius-colliculate. Antenna with 26 flagellomeres; maximum width of flagellum about 2.2 × the minimum width of f1; flagellum blunt, not gradually tapered towards apex. Supra-antennal area ventrally slightly concave, smooth, dorsally colliculate, medially with suture-like longitudinal line ocellar area distinctly convex. Occipital carina almost complete, absent only on short median section of occiput, ventrally joining hypostomal carina at mandible base.

**Mesosoma:** Pronotum longitudinally striate along posterior margin and median transverse sulcus, dorsally coriarius. Mesoscutum coriarius, shiny, with short transverse wrinkles along notaulus. Scuto-scutellar groove distinctly striate. Mesopleuron sparsely pilose, mostly coriarius, dorsal corner longitudinally striate. Subalar ridge narrow, weakly projected, keeled. Mesopleural fovea distinct as a small pit, far from

mesepimeron. Propodeum 1.5 × as long as wide, mostly transversely striate, anterolaterally coriarius, after posterior transverse carina longitudinally striate. Lateral longitudinal carina present as blunt ridge between anterior transverse carinae. Tibiae and tarsi with sparse, small bristles. Fore wing vein 1-Rs+M sinuous, continuous with cross-vein 1m-cu, cross-vein 1m-cu uniformly curved; cross-vein 1cu-a arising slightly distad to base of 1M+Rs; vein 2Cua 2.00 × as long as cross-vein 2cu-a, veins angled at about 130°; APH 1.1; AWH 1.6; HW1C 1.8.

**Metasoma:** T1 mostly coriarius, at midlength with faint longitudinal striae; T1LW 1.6, T1WW 3.35. T2LW 0.60, T2 coriarius, moderately pilose, T2WW 1.4. OST 0.35; ovipositor dorsal valve with four ridge-like teeth; ventral valve subapically with a distinct swelling, without distinct apical teeth.

**Colour:** Dark ferruginous (176,112,025). Head black; mandible light ferruginous, apically blackish; clypeus basally black, lighter towards apex, clypeal margin ferruginous. Scape whitish; pedicel dorsally whitish, ventrally blackish; flagellum basally brownish, apically black, f5–7 and part of f8 whitish. Mesosoma and metasoma dark ferruginous; legs fuscous towards apex; metasoma lighter towards posterior apex, T8, ovipositor and sheath light ferruginous. Wings slightly infusate towards apex.

**Male (Fig. 7C)** Similar to the female except by the following. Fore wing 4.2 mm long; body generally shinier, less pilose and smoother, all sculpturing less pronounced than in female. Triangular lobes on clypeal margin almost indistinct; antenna with 25 flagellomeres, without whitish band; hind tibia more distinctly darker than remainder of legs, uniformly brown; median longitudinal carina of propodeum indistinct, its position marked by a distinct groove instead of carina.

**Variation** Paratype female essentially identical to holotype, except slightly smaller, fore wing 4.6 mm long; lateral longitudinal carina of propodeum weaker.

**Etymology** ‘Perula’ is a Medieval Latin form for ‘pearl’, apparently derived from ‘pernula’, diminutive of ‘perna’ (the brown mussel); in reference to the type locality, Pearl Beach, in Australia. The name is to be treated as a noun in apposition.

**Material examined** 2 ♀♀ 1 ♂. **Holotype** ♀: AUSTRALIA, New South Wales, Pearl Beach, Crommelin Biological Field Station, 33.5511°S, 151.2978°E, sweeping, May 2009, A. Austin (WINC). Condition of type: mounted on triangular point; apical flagellomere of right antenna missing; right hind leg removed for sequencing and glued to separate triangle

point; otherwise intact. *Paratypes*: 1 ♀ 1 ♂, same data as holotype, mounted in triangle point. Paratype female previously used for whole body extraction [‘Extraction Nb. / GS-Cry-378: / whole wasp extracted 2013/14’ // ‘Ichneumonidae/ Ateleute / det S. Klopstein 2014’] – Genbank accession number (as *Ateleute* sp.) KY447113. Both fore legs apicad of coxa detached and glued to the triangle point; right antenna apicad of scape, left mid leg and right ovipositor sheath missing.

*Distribution* Australia.

#### ACKNOWLEDGEMENTS

All the curators mentioned in Material and Methods provided invaluable loans of cryptine specimens. Andrew Bennett (CNCI), Gavin Broad (BMNH) and David Wahl (AEIC) also received the first author in their institutions and loaned all the relevant specimens. Bruno C. de Araújo (ZSM), Helena Onody (MZSP) and Pascal Rousse (MNHN) provided logistic help and good company during BFS’s visits to Munich and Cape Town. Seraina Klopstein (Universität Bern) arranged for the loan from WINC. Research funds were provided by a Doctoral Dissertation Improvement Grant from the U.S. National Science Foundation (Award #1501802); a ‘mini-ARTS’ award from the Society of Systematic Biologists; an Annette Kade Graduate Student Fellowship and a Theodore Roosevelt Memorial Grant, both by the AMNH. The Sackler Institute of Comparative Genomics generously funded much of the DNA sequencing. Simon van Noort was funded by South African NRF (South African National Research Foundation) grants: GUN 2068865; GUN 61497; GUN 79004; GUN 79211; GUN 81139; GUN 98115. The first author was supported by a fellowship from the Richard Gilder Graduate School (AMNH) and is currently supported by the Peter Buck Fellowship Program (NMNH). James Carpenter, Mark Siddall and Lorenzo Prendini (AMNH) provided invaluable guidance and useful comments for this work.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

**Appendix S1.** Full specimen data for terminal taxa used in the phylogenetic analyses. Genbank accession codes to be added as per acceptance of the manuscript. Institutional acronyms are as follows (curators in parentheses). AMNH, American Museum of Natural History, New York, NY, USA (J. Carpenter). BMNH, The Natural History Museum, London, UK (G. Broad). CASC, California Academy of Sciences, San Francisco, CA, USA (R. Zuparko). CNCI, Canadian National Collection of Insects, Arachnids and Nematodes, Ottawa, Canada (A. Bennett). HIC, Hymenoptera Institute Collection, University of Kentucky, Lexington, KY, USA (M. Sharkey). INPA, Instituto Nacional de Pesquisas da Amazônia, Manaus, Brazil (M. Oliveira). MNHN, Muséum National d'Histoire Naturelle, Paris, France (C. Villemant). MUSM, Universidad Nacional Mayor de San Marcos, Lima, Peru (G. Lamas). MZUP, Museu de Zoologia da Universidade de São Paulo, São Paulo, Brazil (C.R.F. Brandão). NHRS, Naturhistoriska Riksmuseet, Stockholm, Sweden (through the Swedish Malaise Trap Program). ROM, Royal Ontario Museum, Toronto, Canada (D. Currie). SAMC, Iziko South African Museum, Cape Town, South Africa (S. van Noort). USUC, Utah State University, Logan, USA (D. Wahl). WINC, Waite Insect and Nematode Collection, Adelaide, Australia (J. Jennings). ZMUT, The Zoological Museum, University of Turku, Helsinki, Finland (I. Sääksjärvi). ZSMC, Zoologische Staatssammlung München (S. Schmidt).

**Appendix S2A.** Maximum likelihood phylogeny of Ateleutinae using the program Gblocks v.0.91b to exclude poorly aligned positions from ribosomal alignments, under default parameters. Numbers at each node correspond to bootstrap values. Nucleotide substitution models are the same as the main analyses except for TVM+G used for 28S.

**Appendix S2B.** Maximum likelihood phylogeny of Ateleutinae using the program Gblocks v.0.91b to exclude poorly aligned positions from ribosomal alignments, under parameters designed to allow for a less stringent selection. Numbers at each node correspond to bootstrap values. Nucleotide substitution models are the same as the main analyses except for TVM+G used for 28S.