DOI: https://doi.org/10.3897/arphapreprints.e76743

Braconidae (Hymenoptera) parasitoid wasps as a model group for turbo taxonomy approaches: lessons from the past and recommendations for the future

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ARPHA Preprints *Author-formatted, not peer-reviewed document posted on 19/10/2021* DOI: https://doi.org/10.3897/arphapreprints.e76743

Braconidae (Hymenoptera) parasitoid wasps as a model group for turbo taxonomy approaches: lessons from the past and recommendations for the future

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Introduction

A recent paper (Sharkey et al. 2021a) describing 416 new species of Braconidae parasitoid wasps (Hymenoptera) from Area de Conservación Guanacaste in Costa Rica has reignited the debate about taxonomic best practices when describing species. The new species were treated in a minimalist way, as stated in the very title of the paper and this quote from their abstract: "Most descriptions consist of a lateral or dorsal image of the holotype, a diagnostic COI consensus barcode, the Barcode Index Number (BINs) code with a link to the Barcode of Life Database (BOLD), and the holotype specimen information required by the International Code of Zoological Nomenclature" (Sharkey et al. 2021a: 2).

Sharkey et al. (2021a) is but the latest example of a growing list of papers that aim to accelerate the description of species on a planet facing a biodiversity crisis in which species may become extinct before they are even described. "Turbo taxonomy" is a catchy name proposed by Butcher et al. (2012) to qualify such papers, and it has been rather enthusiastically applied since then – a Google Scholar search for "turbo taxonomy" retrieved 130 results since 2012 through October 2021. A similar concept "fast-track taxonomy" was proposed by Riedel et al. (2013a) around the same time; I consider them as equivalent and for the sake of simplicity I will use "turbo taxonomy" henceforth.

Although somewhat subjective, turbo taxonomy can be characterized as the rapid description of many species in "fast" produced papers (as compared to the "slower" pace of traditionally produced taxonomic papers). This is usually accomplished using a combination of tools and approaches to automate and expedite dealing with the material examined, e.g., morphological traits quickly assessed and scored, often with brief descriptions and/or descriptions generated using software packages, high-quality illustrations, heavy reliance on molecular and other data (e.g., biological, distributional) to differentiate and diagnose species. The combination of techniques for species recognition and description at least partially intersects with another concept, that of "integrative taxonomy", *sensu* Dayrat (2005), and perhaps sometimes both terms have been used interchangeably – although integrative taxonomy papers are not necessarily "rapidly produced" as is claimed for the turbo taxonomy ones.

The main difference between Sharkey et al. (2021a) relative to previous turbo taxonomy papers, and the reason for present discussions within the scientific community, is that they chose to describe the new species based almost exclusively on DNA barcodes.

Describing new species based only or mostly on molecular data is not new. Hibbett et al. (2011) discussed prospects for sequence-based taxon discovery and description in fungi (see also Taylor 2011, Kõljalg et al. 2013). And Renner (2016) compiled a list of at least 98 names of species of acoels, lichens, angiosperms, annelids, alveolates, arachnids, centipedes, turtles, fishes, butterflies, mollusks, nematodes, and pathogenic fungi that have been published based on diagnostic mitochondrial, plastid, or nuclear DNA substitutions, indels, or rarely genetic distances, with or without the addition of morphological features. Even within Braconidae, some of the coauthors of Sharkey et al. (2021a) had recently published a similar, albeit much smaller paper (Meierotto et al. 2019).

Thus, the novelty of the Sharkey et al. paper is hardly the approach itself but rather the scaling up of the work to a mammoth monograph in which more than 400 new species were described. That is indeed a first. And, as quoted from the very first sentence of their introduction, the authors presented their article as a way

to “further refine methods to overcome the taxonomic impediment of ichneumonoid biodiversity” (Sharkey et al. 2021a: 6).

In the months following that paper, the scientific community has engaged in lively discussions about “how useful” such descriptions are, whether they in fact impede the cataloguing of biodiversity, “how valid” (from the ICZN perspective) those species are, and general issues about the future of taxonomy, shortcomings of BINs and even BOLD (e.g., Ahrens et al. 2021, Engel et al. 2021, Meier et al. 2021).

In this Forum Paper I discuss some of the above issues, present alternative/complementary ideas from my perspective, and include a detailed proposal on how to approach turbo taxonomy in a hyperdiverse group such as braconid parasitoid wasps balancing fast description of species while also keeping a higher use value of the final product(s). I do not claim to have better or newer insights than others, and I certainly do not pretend to have any definitive answers. But perhaps my comments could be useful because a) I am a braconid researcher, like the main authors of the Sharkey et al. (2021a) paper, b) I have published several papers that could be considered as turbo taxonomy and have long been interested in ways to speed up species descriptions, c) I was actually one of the reviewers of Sharkey et al. (2021a) (and for full disclosure, I recommended its acceptance, although I also added many opinions on its taxonomic approach and how it could have been improved, with many of my suggestions being ignored by the authors in the final version), and d) perhaps more importantly, because I think that Sharkey et al. (2021a), even if arguably flawed, demonstrate opportunities that can and should be used by the taxonomic community to improve and speed up work in the future. In that sense, what follows below is less of another critical view of that paper and more of a complementary proposal to improve turbo taxonomic methods.

“Talking the talk and walking the walk” of turbo taxonomy

There are many published papers that discuss the need to and possibilities of speeding up taxonomy by using newer technologies such as DNA barcoding. Unfortunately, most of those papers present somewhat general discussions or are intended just as a proof of concept, without actually applying it to describing new species. In many cases, DNA barcoding is presented as a useful and comparatively fast tool to rapidly distinguish species, often revealing a much higher species diversity than previously thought based on morphological study and/or revealing complexes of cryptic species. However, usually things stop there, and the next step is not made, i.e., the new taxa are not described in those papers praising how much DNA barcoding brings to the taxonomist’s table. I would consider those papers examples of “talking the talk” but not necessarily “walking the walk” (in the sense presented here: https://knowyourphrase.com/talk-the-talk). It is important to stress that this statement does not apply to the four braconid experts and coauthors of the Sharkey et al. (2021a) paper (Michael Sharkey, Scott Shaw, Donald Quicke and Kees van Achteberg) all of whom are world-renowned taxonomists. Altogether they have described more than three thousand new species in hundreds of published papers (e.g., see Yu et al. 2016), and their contributions to our knowledge of Braconidae and other Hymenoptera groups has been outstanding. They have certainly walked the walk!

But the truth is that comparatively few works could have the turbo taxonomy label applied to them. Examples include lichens (Lücking et al. 2017), annelids (Summers et al. 2014), dragonflies (Dijkstra et al. 2015), frogs (Rakotoariso et al. 2017), histers beetles (Caterino & Tishechkin 2013), weevils (Riedel et al. 2013b, 2014, Riedel & Tänzler 2016, Riedel & Narakusumo 2019), and several papers on braconids (Table 1). There is no doubt that other papers than the ones I list can be found in the literature, but they still constitute a minority of published taxonomic revisions. [Papers such as Hartop & Brown (2014) and Srivathsan et al. (2019) could also be considered here, albeit only partially, because they discuss and present novel methodologies for fast description of species (=turbo taxonomy) but only describe one new species each as an example].

What is somewhat surprising (or worrisome?) is the realization that few of the researchers who have published a paper that could be considered as turbo taxonomy have continued to do afterwards, i.e., they have not produced additional monographs in the same turbo taxonomy style. Based on my, admittedly non-exhaustive online searches, I can only mention Riedel and colleagues for weevils (Riedel et al. 2013b, 2014, Riedel & Tänzler 2016, Riedel & Narakusumo 2019) and a series of papers on Braconidae (see Table 1 and discussion below) as two examples of researchers doing turbo taxonomy on a more sustained basis.

One may then ask, if turbo taxonomy is touted as "the way to move forward" in taxonomy, why are there so few adopters of the approach, and even less who repeat their efforts in subsequent papers?

In my opinion the answer is simple: because turbo taxonomy still requires a significant amount of work and time invested, and it is not as easy and rapid as one might think or as it is purported to be in papers advocating for those revolutionary taxonomic approaches.

A simple search of author names reveals that most of the published turbo taxonomy papers have been done primarily by graduate students (M.Sc. and Ph.D.) or postdoctoral fellows. They represent some of the more enthusiastic, hard-working and "overperformer" researchers in the taxasphere, a great combination of youth, energy and a desire/need to advance their careers. They certainly put in the effort needed to accomplish their turbo taxonomy feats, and they deserve all the praise for that. But could those papers become the "new normal" for taxonomy? I would argue that it is unrealistic to expect that turbo taxonomy papers can be produced effortless and quickly, much less in a sustained way –at least those closer to "traditional taxonomy" in the sense of providing keys and morphological descriptions.

I believe that Meierotto et al. (2019), Sharkey et al. (2021a), and others before them (see Introduction for non-Braconidae examples) are probably correct in their claim that a shift of paradigms is possible and needed to increase the speed of taxonomic results. I also agree that DNA-based species recognition should be one of the major driving forces to speed up the cataloguing of biodiversity. Where I disagree with such authors is in the way to implement turbo taxonomy because I believe that this can and should include components other than DNA that increase the "use value" of the paper while not taking much extra time or resources.

Comparing the works of Meierotto and Sharkey with other Braconidae papers of similar size

First let us look at what has been accomplished with turbo taxonomy relative to Braconidae over the past 15 years or so (2005–present). Table 1 presents basic data on some papers, divided in two somewhat arbitrary categories. The first five rows include papers with the largest numbers of treated species (approximately 100–400 species each), to serve as a direct comparison with Sharkey et al. (2021a) which is, by far, the largest paper discussed here. Included are all the large monographs in Braconidae I am aware of that could be considered as examples of turbo taxonomy. The remaining rows contain a sample of papers with fewer treated species overall (approximately 30–80 each), which are comparable in size species-wise with Meierotto et al. (2019). There are certainly more examples of revisions of Braconidae in this second category than what I have listed.

Table 1. Selection of published Braconidae papers (2005-2021) which could be considered as examples of turbo taxonomy. For the sets of data in columns 5–9, the use of "-" means such data was not present in the paper, "+" means that it was used but only in a very basic and limited way, and "++" means that it was fairly used. ACG = Area de Conservación de Guanacaste, Costa Rica.

Paper	Subfamily/ genus Covered	Main geographical area	Total species /new species described	Use of dichotomous keys	Use of morphological data	Use of illustrations	Use of molecular data	Use of other data
Sharkey et al. (2021a)	11 Subfamilies of Braconidae	ACG	416/403	-	-	+	++	+
Marsh et al. (2013)	Doryctinae/ *Heterospilus*	Costa Rica	286/280	++	++	++	-	-
Fernandez-Triana et al. (2014)	Microgastrinae/ *Apanteles*	ACG	205/186	++	++	++	++	++
Butcher et a. (2012)	Rogadinae/ *Aleiodes*	Thailand	186/179	++	++	++	++	-
Arias-Penna et al. (2019)	Microgastrinae/ *Glyptapanteles*	ACG/ Ecuador	136/136	++	++	++	++	++
Liu et al. (2020)	Microgastrinae/ *Apanteles*	China	97/48	++	++	++	-	+
Sharkey et al. (2018)	Agathidinae/ *Alabagrus*	ACG	87/66	++	++	++	++	++
Liu et al. (2019)	Microgastrinae/ *Dolichogenidea*	China	67/39	++	++	++	-	+
Ahlstrom (2005)	Macrocentrinae/ *Macrocentrus*	Nearctic	54/13	++	++	++	-	+
Valerio & Whitfield (2015)	Microgastrinae/ *Hypomicrogaster*	ACG	45/40	++	++	++	-	++
Fernandez-Triana et al. (2014)	Microgastrinae/ *Pseudapanteles*	ACG	36/25	++	++	++	++	++
Liu et al. (2018)	Microgastrinae/ *Dolichogenidea*	China	34/26	++	++	++	-	+
Fernandez-Triana et al. (2015)	Microgastrinae/ *Microplitis, Snellenius*	ACG	33/28	++	++	++	++	++
Meierotto et al. (2019)	Agathidinae/ *Zelomorpha*	ACG	19/18	-	-	+	++	++

Four of the large papers provide identification keys, “traditional” (i.e., morphology based) species descriptions (as opposed to only DNA-based ones), and multiple illustrations of all or most species. The only exception to this is Sharkey et al. (2021a), which does not provide keys or traditional descriptions and includes only a single image per species (usually a lateral habitus). Molecular data to recognize, differentiate and/or describe species was used in all papers except Marsh et al. (2013) and Liu et al. (2020). Other data, mostly biological information, usually host data but also number and shape of wasp cocoons, host plant, microhabitat, etc., were less prevalent, and mostly restricted to those papers treating the Area de Conservación de Guanacaste, Costa Rica (ACG) fauna because of the wealth of biological and ecological information available for Braconidae and other taxa obtained in that area (e.g., Janzen & Hallwachs 2011, 2016, 2020; see also http://janzen.sas.upenn.edu/caterpillars/database.lasso).

The pattern among the shorter papers is mostly similar, with Meierotto et al. (2019) being the only one not to include differential keys or morphological descriptions. All the other papers are more complete from the perspective of morphology, and many also included molecular, biological and ecological data; although, again, the ACG papers were more comprehensive because the authors had access to more information.

An interesting comparison can be drawn between the Meierotto et al. (2019) and Sharkey et al. (2018) papers; both treat a single genus of Agathidinae (Braconidae) but the later is much more comprehensive in its use of features/traits to recognize, identify, and describe the species.

The examples in Table 1 are comprehensive taxonomic revisions that treated dozens and sometimes even hundreds of species each; they included at least some basic morphological data, usually more. Indeed, if a taxon could claim the crown of turbo taxonomy, Braconidae would be a strong candidate. In just one subfamily, Microgastrinae, a total of 720 new species were described between 2014 and 2019 (Fernandez-Triana et al. 2020), the vast majority in papers that would qualify as turbo taxonomy.

There is no question that these papers could have been produced faster and easier if a minimalistic approach, such as those of Meierotto et al. (2019) and Sharkey et al. (2021a), had been adopted. How fast and easy are, however, complicated questions to answer. And how "useful" those papers would be for potential users is an even more difficult one.

Speed, practicality, affordability, democratization of taxonomy and Star Trek

Sharkey et al. (2021a), and for that matter many other papers, my own included, that have treated the ACG fauna benefited immensely from the work previously done by Daniel Janzen, Winnie Halwachs and their team (e.g., Janzen et al. 2009, Janzen & Hallwachs 2011, 2016, 2020). Thanks to the herculean efforts (including their amazing parataxonomists and technicians, mostly in Costa Rica but also in USA and Canada), thousands of specimens have been collected, reared, labelled and databased with recorded host data, and DNA has been extracted, with the available sequences and additional information readily accessible in the Barcode of Life Data System (BOLD). Some of that work is highly technical, and all of it took a lot of time and significant resources, including financial. All or most of that was done before the actual work of the taxonomists started, and in fact was of critical importance or else it would have taken much more time and considerably more resources to produce those taxonomic papers, whether traditional or turbo taxonomy.

Thus, when considering papers that claim to be "fast" because they only rely on DNA-based descriptions, one must also consider "hidden" but significant amounts of work done prior to the taxonomy study. If time, expertise and resources needed to obtain all of the previous information on which the taxonomy is based were accounted for, then those papers would suddenly appear less quick and easy to produce than as advertised, at least relative to ACG studies.

Beyond time and resources not being properly assessed in a paper employing only DNA-based descriptions, there is a bigger issue. And that is the fact that any user of such a paper must, by default, obtain DNA data for their own specimens before any meaningful comparison can be made with the species dealt with in that paper. Otherwise, it is not possible to conclude if a specimen at hand belongs to a previously "DNA-described" species or is new. Thus, "DNA-only description" papers force users to do "DNA-only identifications".

There is no problem with that, say some enthusiastic supporters of turbo taxonomy and DNA barcoding. It will actually democratize taxonomy because technical knowledge of a taxon, including the associated

morphological jargon used to described it (e.g., number of setae on propodeum or sculpture on mesoscutum), would no longer be required. What used to be the domain of a relatively few taxonomists would become mostly unnecessary, because "soon" everyone would be able to use a device, a la "Star Trek" tricorder (https://en.wikipedia.org/wiki/Tricorder), to identify species. It would allow even school children to rapidly identify the caterpillar they found in their backyard or farmers in Central America to recognize which pest or parasitoid wasps are found in their crops. It all looks so nice and promising!

While I have no doubts that technology ultimately will be developed to allow fast, easy and cheap devices to obtain and analyse DNA, and access the comprehensive DNA databases that are necessary to determine whether a specimen at hand represents a described species, that scenario is not yet here (but see Srivathsan et al. 2021 for some new developments that could become viable alternatives in the near future). We are still far from being able to download a "Taxonomy for Dummies" app.

Meanwhile, what we have is the fact that DNA-based taxonomy is not accessible or affordable to everyone (see further analyses and/or other perspectives in Pinheiro et al. 2019, Dupérré 2020, Ahrens et al. 2021, Meier et al. 2021, Srivathsan et al. 2021). At present, it is not possible to obtain a DNA barcode from a single specimen unless the individual has access to a molecular lab, whether this is their own or "one for hire". As an example of the latter, one of the most commonly used such labs, is the Canadian Center for DNA Barcoding (formerly the Biodiversity Institute of Ontario), which charges $1,250 Canadian dollars for a single plate of 95 specimens (http://ccdb.ca/pricing/). However, in addition to that cost, single images of every submitted specimen and an Excel file with some basic information are also required when samples are submitted, which will take additional time and money; also, to consider are shipping costs and dealing with national/international laws regulating access, sharing and exportation of genetic resources.

Never mind the school children or farmers, arguably most world researchers cannot afford the current costs and associated logistic challenges mentioned above to obtain DNA-based identifications for every specimen they may need or want to identify (e.g., Srivathsan et al. 2021). If the route of having to obtain DNA barcodes (or any other molecular marker) to identify species becomes the only route to a scientific name, then this could make taxonomy even less accessible and democratic than using "traditional" techniques such as microscopes and dichotomous keys. At present is certainly valid to argue that the cost of traditional, morphology-based taxonomy is largely a "front end" cost mainly borne by the taxonomist, whereas DNA-only taxonomy necessitates high and significant "back end" user costs.

In addition to cost and who pays this there is also the problem of the almost two million species described in the pre-molecular era, many with no DNA associated. Those species cannot simply be ignored, as it has been claimed to be the case in the Meierotto et al. (2019) paper. Zamani et al. (2020) thoroughly discussed that problem, although Sharkey et al. (2021a, b) gave some counter replies.

In the end, it comes down to the practicality and benefits/damages that minimalistic (extreme?) taxonomic approaches, such as those relying only on DNA barcodes for species description and recognition, bring. Do future revisions to be produced really need to ignore morphology and previously described species to instead rely entirely or almost exclusively on DNA barcodes, with the "justification" of describing species faster because of the biodiversity crisis? Or is it possible to build upon the works of Meierotto et al. (2019), Sharkey et al. (2021a) and others to try finding a middle-of-the-road approach, where speed and practicality are attained while significantly minimizing efforts and cost?

A "cookbook recipe" for turbo taxonomy, including estimated times needed for each task

What I propose below is a workflow and guidelines for preparing turbo taxonomy papers, including estimate times for each task. The main motivation is to provide an alternative to Meierotto et al. (2019) and

Sharkey et al. (2021a) but with the addition of some features that I hope would increase the applicability of the work (from a user perspective) while still maintaining a relatively fast pace. I have based this proposal on my personal experience preparing Braconidae turbo taxonomy papers, but it could be adapted for other taxa, i.e., used like a "cookbook recipe" that can be modified and changed as needed or desired.

I do not pretend to reinvent the wheel, e.g., see Reidel et al. (2013), Hartop & Brown (2014), Srivathsan et al. (2019) for earlier turbo taxonomy proposals and even nicer workflow diagrams (although my proposal includes more detailed analyses of time involved with each task and consideration of other factors). I also strongly recommend checking the new guidelines for species descriptions posted by ZooKeys: https://zookeys.pensoft.net/about#TaxonomicTreatments), which in some ways intersects what I write below. And it may also be fruitful to check the many exchanged messages in the email list for biological systematics Taxacom (http://mailman.nhm.ku.edu/cgi-bin/mailman/listinfo/taxacom), where the Meierotto and Sharkey papers were vigorously discussed in 2019 and 2021 (while I have refrained from commenting on Taxacom about Sharkey et al. (2021a), in 2019 I did share my opinion about Meirotto et al. (2019), and some of the ideas presented here are based on what I wrote to that list at that time).

a) When is it most efficient to use turbo taxonomy approaches?

- The taxon being studied is hyperdiverse, i.e., species-rich, and mostly poorly known, i.e., most species are still undescribed so there are relatively few names not previously associated with DNA data and type material to be considered.
- DNA barcodes are already available for many/most of the species, unless the research project has sufficient resources (time and money) to accomplish this step.
- Databasing of many/most specimens is already available, unless the research project has sufficient resource (time and money) to accomplish this step.
- Imaging equipment is available capable of generating many images in a short period of time and with automated or semi-automated capabilities of stacking images to produce publication-quality images.
- Other sources of data (biological, ecological, etc.) are available for many/most specimens that provide evidence of species status supplemental to DNA/morphology evidence.
- A 'minimum' set of morphological traits to assess specimens is already available, i.e., features have been discussed or proposed in previous studies of the taxon or related taxa by specialist(s) in the taxon in order to provide supplemental evidence of species status and which is necessary for more "traditional" taxonomic approaches. Alternatively, the paper to be produced presents such a set of minimum morphological traits.

b) Species treatment

- New species will be treated, diagnosed and described using a combination of basic morphology (basic key and brief diagnostic description), molecular data when available (e.g., DNA barcodes), ecological/ethological data when available, distribution data, and complete details of the primary type(s) and basic details of all other specimens.
- Previously described species will be incorporated into the paper even if in an incomplete manner due to lack of molecular or other data.

c) Use of morphological data

Simplified key(s) and diagnostic descriptions, with a minimum set of morphological traits will be prepared. The morphological traits, ideally chosen by a specialist in the taxon, need not be numerous but ideally should be easily and quickly assessed and scored (i.e., not requiring dissections, slide preparation or other labour-intensive techniques). It is understood that DNA evidence likely is being used in most turbo taxonomy studies because of a perceived lack of differential morphological features for the group, and that morphology will not necessarily suffice to tell every species. However, morphology should at least be able

to place most (ideally all) species within some sort of smaller group of species. A “species group”, as here considered, is based on some simple trait(s), e.g., “all species with legs brown or black versus all species with legs yellow” and does not necessarily have to be monophyletic.

The morphology component of the taxonomic revision should serve as the minimum piece of information to allow someone with a basic knowledge of the taxonomic group and simple equipment such as a microscope to recognize a species or species group if no other source of information, such as DNA, is available.

Although diagnostic descriptions should be as short as possible based on easily observable features, each species should be illustrated as fully as possible with images showing all body areas and from different angles in order to document the features important for differentiating species in the group (e.g., coloration, sculpture, etc.) and those features that are otherwise not described. Ideally, illustrations should be based on the holotype or specimens compared with the holotype; if a species is thought to be variable morphologically then specimens showing the perceived range in variation should be photographed.

In species complexes with very similar or cryptic morphology, additional effort does not necessarily be spent trying to separate them based on detailed study of morphology or morphometrics, but instead other non-morphological criteria (see below), if known, could be used to help distinguish the species.

The estimated time needed for the morphological work is 5 hours per species. This includes scoring and writing the species description based on minimum morphological traits, and also includes studying intraspecific variation and making a few measurements of relevant structures. All of these steps should take, on average, less than one hour per species, the exception being species with many available specimens and/or significant morphological variation. To account for extremes, an estimate of two hours of work per species is considered here. Photographing a species (4–8 shots of a specimen, to capture different angles) can be done in one hour depending on the number of specimens per species imaged, and the photographic equipment and montaging software used. Preparing a plate of images can be done in less than one hour. Estimating the time to prepare a simplified key is very difficult, here a conservative estimate of one hour per species in the key is proposed.

c) Use of molecular data

DNA barcoding and/or any other molecular marker will be a very important criterion to recognize and diagnose species, and for morphologically cryptic or very similar species, it may be the primary criterion. Species will be characterized as much as possible by their corresponding Barcode Index Number (BIN) (for a definition of BIN see Ratnasingham & Hebert 2013). If a unique BIN does not “work”, i.e., in cases where there is more than one BIN per species or several species share the same BIN, a discussion explaining the rationale to characterize the species molecularly will be necessary.

Where a species is primarily defined and identified by DNA barcodes because, e.g., basic morphology is insufficient or inconclusive, such “DNA-only species” must include sequences from at least two different specimens (to exclude potential definition of a species based on a single sequence, which could be a lab contamination, a chimera, or any other error). Where a species is defined by a combination of traits (morphological, biological, etc.), a less stringent molecular criterion is acceptable, and a single DNA barcode can be sufficient.

The estimated time needed for the molecular tasks is 5 hours per species. Sampling tissue for DNA barcoding from dry, pinned specimens is straightforward and takes less than 10 minutes per specimen. However, the associate requirements for preparing a 96-well plate and submitting it to the lab for processing may require many other tasks, e.g., taking one image per specimen and providing some details of the

specimen for the BOLD database (in the case where specimen tissue is sequenced by the Canadian Center for DNA barcoding). A conservative estimate of 30 minutes per specimen is proposed. Because, as discussed above, it is usually necessary to have DNA barcodes of more than one specimen per species, the estimated here includes 3 hours per species. This estimate will vary significantly if specimens are prepared in batches smaller or larger than one 96-wells plate (which accommodates 95 specimens). Basic analysis of DNA barcodes (Neighbour Joining trees as generated in BOLD) can be done quickly, but more complex and comprehensive analyses will take longer; a conservative estimate of 2 hours per species is proposed here.

d) Use of ecological/ethological data

Any extra information that contributes to recognizing or identifying a species based on ecological or ethological traits should be used as additional evidence supporting species delimitation, but not as the single source to describe a species. Examples in Braconidae include host data, parasitoid ecology, wasp seasonality, etc.

The estimated time needed for the ecological/ethological tasks is 1 hour per species, though this greatly depends on the available information for each taxon; it could be significantly less or even zero. This and the following are probably the least accurate time estimates of the list.

e) Use of distribution data

The minimum standard should be broad geographical distribution, i.e., biogeographical region, country, although detailed locality data is preferable. Information on habitat, e.g., collected in a rainforest or finer details, e.g., collected on understory of forest, on leaves of plant X, should also be provided when available. Distribution data can be used as supplementary evidence supporting a species delimitation and/or recognition, but not as the single source to describe a species.

The estimated time needed for the distribution data task is 1 hour per species, depending on the number of specimens to be data-mined and their geographic breadth, i.e., the amount of data available, and how much of that information is already databased.

f) Dealing with primary type(s) and other specimens.

Details of the name-bearing specimens (primary types) should be provided that minimally meet International Code of Zoological Nomenclature (ICZN) publication requirements, such as location of type depository, but also including specimen unique identifier, specimen sex, country and other information on type specimen label(s) (photos of such labels can be included), and any other detail (e.g., “specimen in good condition” or “missing a leg”) that facilitates the unambiguous recognition of the name-bearing type(s). The ZooKeys guidelines mentioned above are a great standard to follow.

For paratypes and other non-type specimens, considerably abbreviated data can be included. For example, just mentioning the unique identifiers for each specimen instead of detailing all the data for every specimen data is sufficient, as long as the unique identifiers are linked to a publicly available database or dataset where more detailed information is available.

The estimated time needed for dealing with specimen details is 1 hour per species, depending on the number of specimens and prior databasing. If most specimens are already databased, as is becoming more the norm in many collections, then the time may be less than 10 minutes for every primary type and another 10 minutes to record the unique identifiers of all other specimens.

g) Treating previously described species

Previously described species should not be ignored, i.e., all species treated in a new paper should not, by default, be considered as new species if there are prior available names Instead effort should be made to incorporate the previously described species including a reasonable effort to locate and study their types and/or authenticated material. Admittedly, there will be instances when this is not possible and the only data available is just a prior, possibly uninformative and very short description. However, even if only incomplete information is available for previously described species this should be discussed in the paper as far as possible. Two hypothetical examples are discussed below.

The most extreme example would be that of a previously described species known only from the missing holotype, already lost, and a useless original description a few words long. Such a species should still be dealt with in a manner like this: “Species A cannot be run though our key because it is impossible to assess morphological traits X, Y and Z used in the key and the only known specimen is lost. Thus, it is not possible to determine whether the name applies to one of the new species described here, but for practical purposes we assume that is not the case.” Statements like that would make clear to the user/reader that such names cannot be presently assigned, and may never be, while still allowing progress in describing any new species.

Most cases will be less extreme than the above, with most previously described species being able to be placed within some context of the taxonomic revision, i.e., compared with the new species being described. Included should be at least some sort of basic statement such as: “Species B can only be ran to couplet 3 of our key, as characters X and Y (from our key) cannot be assessed for that species, and therefore the name could potentially apply to species C, D or E (new species being described in our paper), but for practical purposes we assume it is none of them”. Again, this method reduces the potential number of names that could (eventually) be found to be synonyms (as at least the species keyed out through the first two couplets would not), while still enabling the new, better characterized species.

In these two hypothetical cases, the previously described species are not ignored –even if their status can never be properly assessed. Thus, the new taxonomic revision would bring together all available information, including presenting the shortcomings and gaps in our current knowledge of some species.

The estimated time needed for dealing with previously described species is, conservatively, 2 hours per species, though it will depend on all factors discussed above.

h) Overall estimate time to deal with one species

The sum of all the time estimates above renders a total of 15 hours per species. That is roughly two days of work per species, or 2.5 species per week. Rounding down to 2 species per week and 50 weeks per year, one arrives at an estimate of 100 new species described in one full-time year of work by a turbo taxonomy practitioner.

However, how accurate is this estimate? Are there examples of this in the real world, or is the above just a theoretical, futile exercise?

It is hard to get actual data from previous turbo taxonomy papers as to the time it took to complete the work because this is rarely (or never) stated by the author(s). But some information is available and other can be guessed.

I have no knowledge of how much time it took Sharkey et al. (2021a) to prepare their paper, but from correspondence with some of the coauthors I know that it took at least two years. Assuming that was the case (and not longer), it would mean a rate of 200 new species per year, an impressive number. But one

needs to factor in how much time was spent by the other three coauthors of that paper that are braconid taxonomists, in addition to the primary author. As such, I suspect that the actual number is below 200 species described per year.

Many of the other larger papers listed in Table 1 represent the work of a Ph.D. thesis or postdoctoral research, each of which probably included at least 3 years of work with the specimens. Based on the total number of species for those revisions, that would give values between 40 and 100 species per year per paper.

Fortunately, I can provide a more accurate estimate for my own work revising *Apanteles* (Braconidae) in Mesoamerica (Fernandez-Triana et al. 2014), which took two years to complete. The revision treated 205 species and at the time I was working full time on the project. Consequently, the pace was roughly 100 species per year. But, very importantly, I benefited greatly from previous work accomplished by Dan Janzen and Winnie Hallwachs in ACG, and some preliminary sorting of species by James Whitfield (University of Illinois at Urbana-Champaign) and his students before I started – all those contributors were rightfully included as coauthors. Thus, the pace to produce that paper is not as fast as it would first appear, and it underscores the difficulties in calculating the actual amount of time it takes to produce comprehensive taxonomic revisions. If anything, I cannot take much credit for the results of that paper (more criticism of my own work below).

Another factor to consider is that a rate of 100 species/year can only be accomplished if treating species "in bulk", i.e., not all groups treated include hundreds of species and a taxonomic revision of "just" a dozen species would not be as time efficient. Furthermore, most people cannot spend 100% of their time doing taxonomic revisions. Even Ph.D. students have other things to do than just taxonomic revisions! Thus, a rate of 100 species/year is, in my opinion, a very high and somewhat unfair standard to expect, much less to meet on a consistent, year to year, basis.

Thus, a rate of 100 species/year is, in my opinion, a very high and somewhat unfair standard to expect, much less to meet on a consistent (i.e., year to year) basis.

However, regardless of the actual time used for any taxonomic revision, efficiencies can be realized, such as including brief descriptions instead of traditional, longer and more comprehensive ones, as proposed above. Going back to the real-world example of my own *Apanteles* paper, for that work I measured and scored 49 morphological characters (altogether more than 15,000 measurements). Many of those characters ultimately proved to be uninformative to distinguish species, being repetitive, too variable, or too subjective or complex to assess. In retrospect, the keys were also unnecessarily long, and some species almost impossible to tell apart based on the keys only (Eduardo Shimbori, personal communication). Looking back, eight years after I completed that paper in 2013, I see many inefficiencies in my work, and much superfluous data that could have been eliminated. Had I chosen a lower number of morphological characters and simplified keys it could have been completed quicker, without scarifying the final quality of the work. Had I assumed an approach similar to my proposed "cookbook recipe" above, the species would have been mostly recognized by DNA and host data, and the keys would have been constructed to serve a more basic and limited function than what I had intended, while still retaining some utility to recognize basic species-groups. [Of course, one could argue that the potential value of any character cannot be comprehended until it has been analyzed. One cannot know that there are "x" number of useful characters, and what they are, prior to studying them. This is what research is all about. Perhaps the "useless" time spent on some measurements is actually an example of what is necessary and a part of all taxonomic revisions, unless morphological features are completely ignored].

One example of how work can be reduced and made faster but still retain value is the case of the *Apanteles leucostigmus* species group, which comprises 39 species and is, by far, the largest and most difficult group

of *Apanteles* to recognize and separate species in Mesoamerica. The key from Fernandez-Triana et al. (2014) for that group (reproduced here in Fig. 1) starts by dealing with a species that cannot be keyed out due to lack of data, with only one specimen known, and is an actual example on how to deal with historical species where information is not available. The remaining 38 species are keyed out using some characters difficult to assess and at some points the differences between halves of the same couplet are very subtle (the paper also included 4–8 images each of the adult wasps for every species.). This key may look good on paper, but in practice it is very difficult and error prone. Indeed, morphology does not work well for this group, which is suspected to include several morphological cryptic species. Instead of that, I could have prepared a much simpler key that only used a few characters relatively easy to assess. Obviously, some species would end in the same point of the key, and thus could only be reliably identified by molecular and biological data. Such a "new" key (Fig. 2) would be much shorter and thus faster to prepare. As for the user of such key, there would still be the need of obtaining DNA barcodes and/or host data to obtain species identifications, but even if the user does not have such data, specimens could still be placed at least in some sub-group.

The above example, which I chose because it was the most difficult and problematic group of the *Apanteles* revision, illustrates how a mostly-but-not-only DNA based paper could be constructed in a more time-effective way. Other *Apanteles* groups from that Fernandez-Triana et al. (2014) revision (and indeed many groups in other taxa) might work even better. The proposed methods could shorten the time to produce a taxonomic revision while still providing some basic elements of more traditional papers.

Concluding remarks

It is very telling to see how many strong reactions a single paper has awaken in just a few months after its publication (or two papers, if we account for Meierotto et al. 2019). For me it has been very interesting and enlightening to read those other colleagues and their reasoning and pleas to avoid a future a la Sharkey et al. (2021a). I strongly recommend the reading of papers such as Pinheiro et al. (2019), Dupérré (2020), Zamani et al. (2020), Ahrens et al. (2021), Engel et al. (2021), Meier et al. (2021), Srivathsan et al. (2021) and references cited there (other papers provide slightly different alternatives or approaches, and are also recommended reading, e.g., Brower (2010), Blaxter (2016), Goulding & Dayrat (2016), Renner (2016), Brown & Wong (2020), Vences (2020); this list is not exhaustive). And to present a more complete and fairer picture, the reader should also consider a second paper by Sharkey et al. (2021b) which tried to provide counterarguments to some of the received criticism (although that paper has also been met with additional counterarguments on its own, e.g., Ahrens et al. (2021), Engel et al. (2021) and Meier et al. (2021)).

The authors cited in the previous paragraph have discussed in a more coherent, compelling and convincing way that I probably could about the dangers and shortcomings of approaches such as those of Meierotto et al. (2019) and Sharkey et al. (2021a). While I agree with most of those arguments, I also think that Meierotto and Sharkey papers provide and opportunity to critically look at and improve our own work. In that sense I prefer to be optimistic and focus on examples and the potential of what could be done (or has already been done by other authors) so that that future turbo taxonomy papers can accomplish the (very much needed) dual goal of being fast and useful for the scientific community and the general public.

ACKNOWLEDGEMENTS

I am very grateful to John Huber and Gary Gibson (CNC) for their excellent reviews of earlier versions of the paper, which considerably improved the manuscript. This work was supported by Project J-002276

"Systematics of beneficial arthropods in support of resilient agroecosystems", from Agriculture and Agri-Food Canada.

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FIGURE CAPTIONS

Figure 1. Details of the key to the *Apanteles leucostigmus* species-group as it appeared in Fernandez-Triana et al. (2014). The plate shows a composite image of the key in the same format it appeared in the online version of that key (https://zookeys.pensoft.net/articles.php?id=3394).

Figure 2. Details of the key to the *Apanteles leucostigmus* species-group as it would look based on modifications detailed in the present paper (see section "h) Overall estimate time to deal with one species" in the current manuscript).

Key to species of the *leucostigmus* group

The species ***Apanteles albinervis***, included in this group because of its morphology, is only known from the male holotype, and our key is only to females. There are no hosts or molecular data available for the holotype, collected in "Mexico" in 1904. It is therefore impossible to key this species by any of the character systems used here.

1	Metatibia entirely or mostly (>0.7) dark brown to black, with yellow to white usually restricted to anterior 0.2 at most (rarely with pale area extending up to anterior 0.3 of metatibia) (as in **Figs 166a, d**)	2
–	Metatibia light yellow to orange-yellow from 0.4 to almost entire metatibia (as in **Figs 197c, 200c**)	26
2(1)	Ovipositor sheaths at least 1.0 × as long as metatibia and 1.3 × as long as metafemur	3
–	Ovipositor sheaths at most 0.9 × as long as metatibia and 1.1 × as long as metafemur	4
3(2)	T1 length 2.7–2.8 × its width at posterior margin; T1 maximum width 1.6–1.7 × its width at posterior margin; metafemur usually more than 3.0 × as long as wide (rarely 2.8–2.9 ×) [Host species *Codatractus imalene*]	***Apanteles luzmariaromeroae*** Fernández-Triana, sp. n.
–	T1 length 2.5–2.6 × its width at posterior margin; T1 maximum width 1.4–1.5 × its width at posterior margin; metafemur 2.8 × as long as wide [Host species *Astraptus talus*]	***Apanteles marcovenicioi*** Fernández-Triana, sp. n. (N = 1)
4(2)	Ovipositor at most 0.7 × as long as metatibia and 0.8 × as long as metafemur	5
–	Ovipositor more than 0.7 × as long as metatibia and usually more than 0.8 × as long as metafemur	6
5(4)	Larger species, body length usually 2.3-2.5 mm (rarely 2.1 mm), and fore wing length usually 2.5–2.6 mm (rarely 2.3–2.4 mm); T1 length 2.7–2.8 × its width at posterior margin [Host species: *Bungalotis erythus*]	***Apanteles ciriloumanai*** Fernández-Triana, sp. n.
–	Smaller species, body length at most 2.1 mm, and fore wing length at most 2.3 mm; T1 length 2.5-2.6 × its width at posterior margin [Host species: *Nascus* spp.]	***Apanteles josecortesi*** Fernández-Triana, sp. n.
6(4)	Metafemur at most 2.8 × as long as wide (rarely 2.9 × in individual specimens), ***and*** ovipositor sheaths less than 0.9 × as long as metafemur	7
–	Metafemur at least 2.9 × as long as wide ***and/or*** ovipositor sheaths at least 0.9 × as long as metafemur	9
7(6)	Fore wing length 2.5–2.6 mm and body length at least 2.3 mm (usually more) [Host species: *Ocyba calathana*. A total of 18 diagnostic characters in the barcoding region: 38 C, 55 C, 61 C, 154 C, 235 T, 310 C, 316 T, 322 T, 358 C, 397 C, 405 G, 431 C, 457 C, 476 C, 604 T, 610 C, 637 A, 641 C]	***Apanteles cynthiacorderoae*** Fernández-Triana, sp. n.
–	Fore wing length at most 2.4 mm (usually less) and body length usually less than 2.3 mm [Host species: *Cephise aelius* or *Phocides* spp. A total of 18 diagnostic characters in the barcoding region: 38 T, 55 T, 61 T, 154 T, 235 C, 310 T, 316 A, 322 A, 358 T, 397 T, 405 A, 431 A, 457 T, 476 A, 604 A, 610 T, 637 T, 641 T]	8
8(7)	T1 length 2.3–2.8 × its width at posterior margin (rarely 2.1–2.2 ×) [Host species: *Cephise aelius*. A total of 39 diagnostic characters in the barcoding region: 19 T, 43 A, 49 C, 98 A, 118 C, 170 A, 181 G, 184 A, 187 T, 212 C, 238 T, 259 C, 263 T, 284 C, 295 A, 298 A, 304 T, 340 C, 364 T, 379 T, 400 C, 421 T, 439 C, 448 T, 458 T, 490 C, 507 T, 508 T, 529 C, 536 T, 562 A, 574 A, 578 T, 589 T, 601 C, 616 T, 629 T, 646 T, 652 C]	***Apanteles hazelcambroneroae*** Fernández-Triana, sp. n.
–	T1 length 2.1–2.2 × its width at posterior margin [Host species: *Phocides* spp. A total of 39 diagnostic characters in the barcoding region: 19 C, 43 T, 49 T, 98 G, 118 T, 170 G, 181 A, 184 T, 187 C, 212 T, 238 C, 259 T, 263 C, 284 T, 295 T, 298 G, 304 C, 340 T, 364 A, 379 C, 400 T, 421 C, 439 T, 448 C, 458 C, 490 T, 507 C, 508 C, 529 T, 536 C, 562 T, 574 T, 578 C, 589 C, 601 T, 616 C, 629 C, 646 C, 652 T]	***Apanteles randallgarciai*** Fernández-Triana, sp. n.
9(6)	Fore wing with veins C+Sc+R and R1 mostly brown; usually veins r, 2RS, 2M, (RS+M)b, 1CU, 2Cua, and 1m-cu partially brown; interior area of other veins, and at least part of pterostigma, usually light brown or yellowish-white (as in **Figs 165b, 172b, 189b**)	10
–	Fore wing with veins C+Sc+R and R1 with brown coloration restricted narrowly to borders, interior area of those veins and pterostigma (and sometimes veins r, 2RS and 2M) transparent or white; other veins mostly transparent (as in **Figs 173b, 174b, 175b**)	19
10(9)	Metafemur 2.7 × as long as wide; ovipositor sheaths 0.9 × as long as metatibia and 1.1 × as long as metafemur	***Apanteles eugeniaphilipsae*** Fernández-Triana, sp. n. (N = 2)
–	Metafemur at least 2.8 × as long as wide; ovipositor sheaths at most 0.8 × (rarely 0.9 ×) as long as metatibia and at most 1.0 × as long as metafemur	11
11(10)	Maximum width of T1 (at about 0.7–0.8 × its length) more than 1.7 × its width at posterior margin	***Apanteles rodrigogamezi*** Fernández-Triana, sp. n.
–	Maximum width of T1 (at about 0.7–0.8 × its length) less than 1.6 × its width at posterior margin	12
12(11)	Maximum width of T1 (at about 0.7–0.8 × its length) usually at most 1.2 × its width at posterior margin; T1 appearing almost parallel-sided	***Apanteles gerardobandoi*** Fernández-Triana, sp. n.
–	Maximum width of T1 at least 1.3 × its width at posterior margin; T1 clearly appearing to widen from base to 0.7–0.8 × its length, then narrowing towards posterior margin of mediotergite	13
13(12)	Ovipositor sheaths about 0.44 mm, metafemur 0.47 mm, metatibia 0.59 mm, and maximum width of T1 0.18 mm, much shorter than below; body length 1.9–2.0 mm and fore wing 2.1–2.2 mm	***Apanteles ricardocaleroi*** Fernández-Triana, sp. n.
–	Ovipositor sheaths 0.49–0.59 mm, metafemur 0.54–0.59 mm, metatibia 0.63–0.72 mm and maximum width of T1 0.20–0.25 mm, much longer than above; body length and fore wing usually larger than 2.2 mm, very rarely smaller	14
14(13)	Ovipositor sheaths at most 2.0 × (rarely 2.3 ×) as long as maximum width of T1	***Apanteles diniamartinezae*** Fernández-Triana, sp. n.
–	Ovipositor sheaths at least 2.4 × as long as maximum width of T1	15
15(14)	Host species: *Calliades zeutus* or *Urbanus dorysus*	16
–	Hosts species: *Telemiades* spp. (one single rearing record from *Phocides lilea*)	17
16(15)	Body length 1.9–2.0 mm; fore wing 2.1–2.2 mm [Host species: *Calliades zeutus*. A total of 23 diagnostic characters in the barcoding region: 30 C, 66 G, 75 G, 84 T, 138 T, 147 A, 192 T, 219 T, 264 A, 315 A, 352 C, 378 T, 388 A, 397 T, 414 A, 420 C, 528 C, 535 T, 547 T, 561 T, 627 T, 639 C, 645 C]	***Apanteles pablomunanai*** Fernández-Triana, sp. n.
–	Body length 2.3 mm or more (rarely 2.1 mm); fore wing at least 2.5 mm [Host species: *Urbanus dorysus*. A total of 23 diagnostic characters in the barcoding region: 30 T, 66 A, 75 A, 84 C, 138 C, 147 G, 192 C, 219 C, 264 G, 315 T, 352 T, 378 C, 388 G, 397 G, 414 G, 420 A, 528 T, 535 C, 547 C, 561 A, 627 A, 639 T, 645 T]	***Apanteles josemonteroi*** Fernández-Triana, sp. n.
17(15)	Host species: *Telemiades oiclus*. A total of 10 diagnostic characters in the barcoding region: 57 G, 144 T, 264 G, 273 C, 276 T, 339 C, 381 G, 477 T, 525 C, 645 C	***Apanteles carlosvlquezi*** Fernández-Triana, sp. n.
–	Hosts species: *Telemiades fides* (one single rearing record from *Phocides lilea*). A total of 10 diagnostic characters in the barcoding region: 57 A, 144 C, 264 A, 273 T, 276 A, 339 T, 381 A, 477 A, 525 T, 645 T	18
18(17)	A total of 18 diagnostic characters in the barcoding region: 73 C, 99 A, 205 C, 265 T, 270 T, 286 C, 315 T, 321 A, 358 T, 462 C, 489 T, 528 T, 535 T, 541 T, 564 T, 567 T, 573 A, 624 A,	***Apanteles inesolisae*** Fernández-Triana, sp. n.
–	A total of 18 diagnostic characters in the barcoding region: 73 T, 99 G, 205 T, 265 C, 270 C, 286 T, 315 A, 312 T, 358 C, 462 T, 489 C, 528 C, 535 C, 541 C, 564 A, 567 C, 573 C, 624 T	***Apanteles manuelzumbadoi*** Fernández-Triana, sp. n.
19(9)	Ovipositor sheaths 0.6–0.8 × (average 0.7 ×) as long as metatibia and 0.8–0.9 × as long as metafemur	20
–	Ovipositor sheaths 0.8–0.9 × (average at least 0.8 ×) as long as metatibia and at least 1.0 × as long as metafemur	21
20(19)	Antenna same length or longer than body; T1 length usually less than 2.3 × its width at posterior margin; ovipositor sheaths 0.7–0.8 × as long as metatibia and 0.8–1.0 × as long as metafemur	***Apanteles raulsolorsanoi*** Fernández-Triana, sp. n.
–	Antenna shorter than body; T1 length 2.5–2.6 × its width at posterior margin; ovipositor sheaths 0.5–0.6 × as long as metatibia and 0.7–0.8 × as long as metafemur	***Apanteles juanmatai*** Fernández-Triana, sp. n.
21(19)	Host species: *Aguna* spp	22
–	Host species: either *Bungalotis*, *Chioides*, *Polygonus*, *Telemiades*, or *Urbanus*	23
22(21)	Metatibia almost entirely dark brown to black, with yellow to white coloration restricted to anterior 0.1 at most; T1 length 2.3–2.4 × its width at posterior margin; T1 maximum width 1.2–1.3 × its width at posterior margin	***Apanteles minorcarmonai*** Fernández-Triana, sp. n.
–	Metatibia with anterior 0.3 yellow; T1 length 2.9 × or more its width at posterior margin; T1 maximum width 1.8–1.9 × its width at posterior margin	***Apanteles jesusugaldei*** Fernández-Triana, sp. n.
23(21)	Antenna clearly shorter than body length, usually 0.8–0.9 × as long as body; metatibia with anterior 0.3 yellow (a few specimens may have metatibia anterior 0.5 yellow, and will not run through here)	24
–	Antenna as long or slightly longer than body length; metatibia almost entirely dark brown to black, with yellow to white coloration restricted to anterior 0.1 at most	25
24(23)	T1 length more than 3.0 × its width at posterior margin; T1 maximum width 1.8–1.9 × its width at posterior margin [Host species: *Urbanus* spp.]	***Apanteles eliethcantillanoae*** Fernández-Triana, sp. n.
–	T1 length 2.3–2.4 × its width at posterior margin; T1 maximum width 1.4–1.5 × its width at posterior margin [Hosts species: *Chioides zilpa*, *Polygonus leo*]	***Apanteles federicomatarritai*** Fernández-Triana, sp. n.
25(23)	Body length 2.3–2.6 mm (rarely 2.1–2.2 mm); fore wing length at least 2.5 mm; metafemur length 2.7–3.0 × its width [Host species: *Bungalotis quadratum*]	***Apanteles alvarosugaldei*** Fernández-Triana, sp. n.
–	Body length 2.1–2.2 mm); fore wing length 2.3–2.4 mm; metafemur length 3.2–3.3 × its width [Host species: *Telemiades fides*]	***Apanteles johanvargasi*** Fernández-Triana, sp. n. (N =3)
26(2)	Metatibia almost entirely yellow, at most with posterior 0.1 brown or just with slightly darker spot which is almost same color than rest of metatibia	27
–	Metatibia with posterior 0.3–0.4 dark brown, clearly darker than rest of metatibia	31
27(26)	Ovipositor sheaths averaging 0.44 mm (range 0.40–0.46 mm), their length 0.6–0.7 × metatibia length and 0.7–0.8 × metafemur length	***Apanteles mariachavarriae*** Fernández-Triana, sp. n.
–	Ovipositor sheaths usually over 0.50 mm (***if*** rarely 0.45 mm in length, ***then*** species average over 0.48 mm), ovipositor sheaths 0.8 × metatibia length (rarely 0.7 ×) and 0.9–1.0 × as long as metafemur	28
28(27)	Antenna shorter than body; T1 length 2.7–2.8 × its width at posterior margin; T1 maximum width 1.6–1.7 × its width at posterior margin	***Apanteles duvalierbricenoi*** Fernández-Triana, sp. n.
–	Antenna at least as long as body; T1 length 2.3-2.4 × its width at posterior margin; T1 maximum width 1.4–1.5 × its width at posterior margin	29
29(28)	Host species: *Astraptes anaphus*. A total of 14 diagnostic characters in the barcoding region: 73 T, 145 C, 193 T, 265 A, 293 A, 316 A, 343 G, 359 C, 401 C, 421 T, 476 C, 562 T, 571 C, 628 T	***Apanteles sigilfredomarini*** Fernández-Triana, sp. n.
–	Host species: *Urbanus* spp. (in two rare cases *Astraptes alardus*, Dan check that for species Rodriguez24). A total of 14 diagnostic characters in the barcoding region: 73 C, 145 T, 193 C, 265 G, 293 T, 316 T, 343 A, 359 T, 401 T, 421 A, 476 A, 562 A, 571 T, 628 A	30
30(29)	Host species: *Urbanus simplicius*. A total of four diagnostic characters in the barcoding region: 166 G, 232 C, 373 T, 379 T	***Apanteles sergioriosi*** Fernández-Triana, sp. n.
–	Host species: *Urbanus dorantes* (plus 2 *Astraptes* records). A total of four diagnostic characters in the barcoding region: 166 A, 232 A, 373 A, 379 C	***Apanteles ronaldzunigai*** Fernández-Triana, sp. n.
31(26)	Fore wing with veins C+Sc+R and R1 mostly brown; usually veins r, 2RS, 2M, (RS+M)b, 1CU, 2Cua, and 1m-cu partially brown; interior area of other veins, and at least part of pterostigma, usually light brown or yellowish-white (as in **Figs 165b, 172b, 189b**)	32
–	Fore wing with veins C+Sc+R and R1 with brown coloration restricted narrowly to borders, interior area of those veins and pterostigma (and sometimes veins r, 2RS and 2M) transparent or white; other veins mostly transparent (as in **Figs 173b, 174b, 175b**)	33
32(31)	Ovipositor sheaths 0.8 × as long as metatibia and 1.0 × as long as metafemur; T1 length 2.7–2.8 × its width at posterior margin [Host species: *Urbanus dorysus*]	***Apanteles lilliammenae*** Fernández-Triana, sp. n.
–	Ovipositor sheaths 0.5 × as long as metatibia and 0.6 × as long as metafemur; T1 length 2.3–2.4 × its width at posterior margin [Host species: *Urbanus dorantes*, *Urbanus teleus*]	***Apanteles wadyobandoi*** Fernández-Triana, sp. n.
33(31)	Ovipositor sheaths 0.7 × as long as metatibia ***and*** 0.7–0.8 × as long as metafemur; metafemur 3.2 × as long as wide	34
–	Ovipositor sheaths usually 0.8 × as long as metatibia (rarely 0.7 ×) ***and*** 0.9–1.0 × as long as metafemur; metafemur usually less than 3.0 × as long as wide (rarely up to 3.2 ×)	35
34(33)	Body length at most 2.2 mm and fore wing length at most 2.4 mm; metafemur at most 2.9 × as long as wide; T1 length less than 2.0 × its width at posterior margin [Host species: *Urbanus proteus*. Distribution: Caribbean islands (Cuba, Grenada, Puerto Rico, St. Vincent), and southern United States (Florida)]	***Apanteles leucostigmus*** (Ashmead, 1900)
–	Body length at least 2.5 mm and fore wing length at least 2.7 mm; metafemur at least 3.2 × as long as wide; T1 length more than 2.6 × its width at posterior margin [Host species: mostly *Astraptes* spp., four known records of *Urbanus* spp. (all different species than *Urbanus proteus*). Distribution: Costa Rica (ACG)]	***Apanteles jorgehernandezi*** Fernández-Triana, sp. n.
35(33)	T1 length 1.9–2.0 × its width at posterior margin [Host species: Mostly *Urbanus albimargo* and *Urbanus dorysus* (rarely also *Autochton* sp.). A total of 19 diagnostic characters in the barcoding region: 54 C, 99 A, 177 C, 186 C, 216 T, 237 T, 330 T, 343 A, 388 C, 387 T, 396 A, 423 T, 460 A, 461 T, 528 T, 534 T, 558 A, 580 T, 606 G]	***Apanteles rostermoragai*** Fernández-Triana, sp. n.
–	T1 length 2.3–2.6 × its width at posterior margin [Host species: Mostly *Achalarus*, *Astraptus*, *Cogia* and *Thessia*; if from genus *Urbanus*, then almost always from other species than above (*Urbanus belli*, *Urbanus dorantes*, *Urbanus teleus* and *Urbanus viterboana*; very rarely from *Urbanus albimargo*). Barcoding region with different nucleotides at positions mentioned in first half of couplet]	36
36(35)	T1 length 2.5–2.6 × its width at posterior margin; T1 maximum width 1.6–1.7 × its width at posterior margin [Host species: *Urbanus albimargo*, and rarely from *Achalarus toxeus*, *Cogia calchas* and *Thessia jalapus*. A total of 10 diagnostic characters in the barcoding region: 57 C, 93 C, 111 T, 117 G, 150 T, 177 A, 183 T, 309 A, 4444 T, 606 C]	***Apanteles angelsolisi*** Fernández-Triana, sp. n.
–	T1 length 2.3–2.4 × its width at posterior margin; T1 maximum width 1.4–1.5 × its width at posterior margin [Host species: *Astraptes* spp., and *Urbanus* spp. but not *Urbanus albimargo*. Barcoding region with different nucleotides at positions mentioned in first half of couplet]	37
37(36)	Metafemur length usually less than 3.0 × its width (range: 2.8–3.1 ×); fore wing length 2.2–2.5 mm [Host species: *Urbanus belli* (with one record of *Urbanus viterboana*). A total of five diagnostic characters in the barcoding region: 192 G, 225 T, 279 C, 615 C, 685 T]	***Apanteles gladysrojasae*** Fernández-Triana, sp. n.
–	Metafemur length usually more than 3.0 × its width (range: 3.0–3.4 ×); fore wing length 2.5–2.7 mm [Host species: Mostly species of *Astraptes* (*Astraptes alardus*, *Apanteles apastus*, *Astraptes brevicauda*, *Astraptes talus*, *Astraptes tucuti*), with one record of *Urbanus belli*. Barcoding region with different nucleotides at positions mentioned in first half of couplet]	***Apanteles bernardoespinozai*** Fernández-Triana, sp. n.

1 Metatibia entirely or mostly (>0.7) dark brown to black, with yellow to white usually restricted to anterior 0.2 at most (rarely with pale area extending up to anterior 0.3 of metatibia) (as in Figs 166a, d) 2
– Metatibia light yellow to orange-yellow from 0.4 to almost entire metatibia 4

2(1) Ovipositor sheaths at least 1.0 × as long as metatibia and 1.3 × as long as metafemur .....
Apanteles luzmariaromeroae [Host: *Codatractus imalena*] [DNA barcode]
Apanteles marcovenicioi [Host *Astraptus talus*] [DNA barcode]
– Ovipositor sheaths at most 0.9 × as long as metatibia and 1.1 × as long as metafemur 3

3(2) Fore wing with veins C+Sc+R and R1 mostly brown; usually veins r, 2RS, 2M, (RS+M)b, 1CU, 2Cua, and 1m-cu partially brown; interior area of other veins, and at least part of pterostigma, usually light brown or yellowish-white .....
Apanteles josecortesi [Host: *Nascus* spp.] [DNA barcode]
Apanteles eugeniaphilipsae [*Narcosius samzon*] [DNA barcode]
Apanteles rodrigogamezi [Host: *Bungalotis diophorus*][DNA barcode]
Apanteles gerardobandoi [Host: *Telemiades fides*] [DNA barcode]
Apanteles ricardocaleroi [Hosts: *Aguna asander*, *A. panama*, *A. arunce hypozonius*] [DNA barcode]
Apanteles diniamartinezae [Hosts: *Astraptes augeas*, *A. obstupefactus*, *A. syncedoche*, *A. inflatio*, *A. fruticibus*] [DNA barcode]
Apanteles pabloumanai [Host: *Calliades zeutus*] [DNA barcode]
Apanteles josemonteroi [Host: *Urbanus doryssus*] [DNA barcode]
Apanteles carlosviquezi [Host: *Telemiades oielus*] [DNA barcode]
Apanteles inesolisae [Hosts: *Telemiades antiope*, *T. fides*] [DNA barcode]
Apanteles manuelzumbadoi [Host: *Telemiades fides*] [DNA barcode]
– Fore wing with veins C+Sc+R and R1 with brown coloration restricted narrowly to borders, interior area of those veins and pterostigma (and sometimes veins r, 2RS and 2M) transparent or white; other veins mostly transparent .....
Apanteles ciriloumanai [Host: *Bungalotis erythus*] [DNA barcode]
Apanteles cynthiacorderoae [Host: *Ocyba calathana*] [DNA barcode]
Apanteles hazelcambroneroae [Host: *Cephise aelius*] [DNA barcode]
Apanteles randallgarciai [Hosts: *Phocides* spp.] [DNA barcode]
Apanteles raulsolorsanoi [Host: *Narcosius helen*] [DNA barcode]
Apanteles juanmatai [Host: *Phocides lilea*] [DNA barcode]
Apanteles minorcarmonai [Host: *Aguna* sp. Burns01] [DNA barcode]
Apanteles jesusugaldei [Host: *Aguna* sp. Burns02] [DNA barcode]
Apanteles eliethcantillanoae [Host: *Urbanus* spp.] [DNA barcode]
Apanteles federicomatarritai [Hosts: *Chioides zilpa*, *Polygonus leo*] [DNA barcode]
Apanteles alvarougaldei [Host: *Bungalotis quadratum*] [DNA barcode]
Apanteles johanvargasi [Host: *Telemiades fides*] [DNA barcode]

4(1) Metatibia almost entirely yellow, at most with posterior 0.1 brown or just with slightly darker spot which is almost same color than rest of metatibia .....
Apanteles mariachavarriae [Host: *Urbanus teleus*] [DNA barcode]
Apanteles duvalierbricenoi [Host: *Urbanus dorantes*] [DNA barcode]
Apanteles sigifredomarini [Host: *Astraptes anaphus*] [DNA barcode]
Apanteles sergioriosi [Host: *Urbanus simplicius*] [DNA barcode]
Apanteles ronaldzunigai [Hosts: *Urbanus dorantes* and 2 *Astraptes* records] [DNA barcode]
– Metatibia with posterior 0.3–0.4 dark brown, clearly darker than rest of metatibia .....
Apanteles lilliammenae [Host: *Urbanus doryssus*] [DNA barcode]
Apanteles wadyobandoi [Host: *Urbanus dorantes*, *Urbanus teleus*] [DNA barcode]
Apanteles leucostigmus [Host: *Urbanus proteus*] [DNA barcode]
Apanteles jorgehernandezi [Hosts: mostly *Astraptes* spp., four known records of *Urbanus* spp. (all different han *Urbanus proteus*)] [DNA barcode]
Apanteles rostermoragai [Host: Mostly *Urbanus albimargo* and *U. doryssus* (rarely *Autochton* sp.] [DNA barcode]
Apanteles angelsolisi [Host: *Urbanus albimargo*, rarely *Achalarus toxeus*, *Cogia calchas* and *Theszia jalapus*] [DNA barcode]
Apanteles gladysrojasae [Host: *Urbanus belli* (one record of *Urbanus viterboana*] [DNA barcode]
Apanteles bernardoespinozai [Host: *Astraptes alardus*, *A. brevicauda*, *A. talus*, *A. tucuti*, *Narcosius samzon*, *Urbanus belli*, *U. dorantes*, *U. doryssus*] [DNA barcode]