# Eight new species and an annotated checklist of Microgastrinae (Hymenoptera, Braconidae) from Canada and Alaska 

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#### Abstract

Based on the study of $12,000+$ specimens, an annotated checklist of 28 genera and 225 species of Microgastrinae braconids from Canada and Alaska is provided, increasing by $50 \%$ the number of species for the region. The genera Distatrix, Iconella, Protomicroplitis and Pseudapanteles for Canada, and Diolcogaster for Alaska are recorded for the first time; all but Iconella and Protomicroplitis represent the northernmost extension of their known distribution. Eight new species are described: Apanteles huberi sp.n., A. jenniferae sp.n., A. masmithi sp.n., A. roughleyi sp.n., A. samarshalli sp.n., Distatrix carolinae sp.n., Pseudapanteles gouleti sp.n., and Venanus heberti sp.n. For the more diverse genera, especially Cotesia, Microplitis, Apanteles, Dolichogenidea and Glyptapanteles, many more species are expected to be found. DNA barcode sequences (cytochrome c oxidase I, or CO1) for $3,500+$ specimens provided an additional layer of useful data. CO1 sequences were incorporated to the new species descriptions whenever possible, helped to clarify the limits of some species, and flagged cases where further study is needed. Preliminary results on the latitudinal gradient of species/genera richness $\left(45-80^{\circ} \mathrm{N}\right)$; as well as biogeographical affinities of the Canadian/Alaska fauna, are discussed. Taking into account the number of specimens in collections still to be studied, data from the barcoded specimens, and extrapolations from Lepidoptera diversity (the host group of the subfamily) the actual diversity of Microgastrinae in the region is estimated to be at least twice that currently known.


## Keywords

Microgastrinae, Canada, Alaska, new species, checklist, DNA barcoding, diversity

## Introduction

Microgastrinae are the single most important group of Lepidoptera parasitoids (Whitfield 1995, 1997), and with over 2,000 described species, rank as the second most diverse subfamily of Braconidae (Yu et al. 2005; Jones et al. 2009). The actual diversity of the group has been estimated at 4,000-10,000 species worldwide (e.g. Mason 1981; Dolphin and Quicke 2001; Jones et al. 2009).

The Catalogue of Nearctic Hymenoptera (Marsh 1979) recorded 124 species of Microgastrinae in Canada and Alaska, a number that 30 years later had increased to 150 (data compiled after Yu et al. 2005; Fernández-Triana et al. 2009b). However, those numbers represent just a fraction of the actual diversity of the group, a fact that has become more evident recently with the examination of extensive material collected throughout the region and the advent of new techniques (such as DNA barcoding) that have been made available for the study of the subfamily.

In this paper eight new species are described; and an updated checklist of the Canadian and Alaskan Microgastrinae is provided with known distribution, taxonomic and/or biological comments when necessary.

## Methods

This study is based mostly on the study of the Microgastrinae housed in the Canadian National Collection of Insects (CNC). CNC is one of the largest collections of the group in the world with over 100,000 pinned specimens plus many thousands more in alcohol (Fernández 2007). The scope of the CNC is worldwide but the strongest representation is from the Nearctic, especially Canada. More than 11,000 Canadian specimens and around 1,000 from Alaska were reviewed, but a significant amount of material still awaits study.

Other collections (curator names provided between brackets), were partially studied and their data were used to compile the distribution of species by provinces.:

- Great Lakes Forestry Centre, Sault Ste Marie, ON [Kevin Barber, Kathryn Nystrom]. A few hundred specimens reared from Choristoneura spp. (Tortricidae), and from Lepidoptera on blueberry. Geographical scope: mostly ON.
- J. B. Wallis Museum, University of Manitoba, Winnipeg, MB [Rob Roughley]. A few dozen specimens. Geographical scope: MB and SK.
- Laurentian Forestry Centre, Ste.-Foy, QC [Jan Klimaszewski, Karine Savard]. A few hundred specimens, many of them reared. Geographical scope: QC.
- Lyman Museum, McGill University, Montreal, QC [Stephanie Boucher]. Around 400 specimens. Geographical scope: Canada.
- Northern Forestry Centre, Edmonton, AB [David Langor, Daryl Williams]. A few hundred specimens, many of them reared. Geographical scope: AB, NL.
- University of Guelph Insect Collection, Guelph, ON [Steve Marshall]. A few hundred specimens. Geographical scope: ON.
- University of Fairbanks, AK [Derek Sikes, Matthew Bowser]. All Microgastrinae (few dozen specimens). Geographical scope: AK.
- University of Toronto, Faculty of Forestry, Toronto, ON [Sandy Smith, Laura Timms, Nurul Islam]. Around 400 specimens were studied. Geographical scope: ON.
- Pacific Forestry Centre, Victoria, BC [Imre Otvos]. Several thousand air-dried specimens in gelatin capsules, reared from Choristoneura spp. were checked with one hundred randomly selected and mounted for further study. Geographical scope: BC.

Whitfield (1995) provided a much needed updated list of the Nearctic Microgastrinae, and assigned to genus all species from the region not treated by Mason (1981). Van Achterberg (2002b) proposed a radical reduction in the number of Microgastrinae genera, and re-arranged all western Palearctic species accordingly (some of those species are also found in Canada and/or Alaska). His modifications were incorporated in the Ichneumonoidea section of Taxapad (Yu et al. 2005), and also the Fauna Europaea website (van Achterberg 2004). Although certainly valid in some regards, van Achterberg (2002b) was based mostly on Holarctic species and contains some decisions not fully supported by additional data (as stated in his paper, more details were intended to be provided later, but there are no published developments to date). Until a study of the microgastrine fauna at world level is available, it seems premature to adopt van Achterberg's classification (Broad et al. 2009). Therefore, here I am following Whitfield (1995) as the standard for generic and species limits for the Nearctic. The only exceptions are: Dolichogenidea breviventris (Ratzeburg, 1848), where I am following Papp (1978); and Glyptapanteles pallipes (Reinhard, 1880), where I am following Papp (1983). Those two cases are further explained in the annotated checklist.

The new species described in this paper are of importance in biological control efforts ( 3 species of Apanteles (Fernández-Triana and Huber 2010)), represent the northernmost record of two genera (one species each of Distatrix and Pseudapanteles), are bizarre species (one Apanteles) or illustrate the potential of integrating barcoding with traditional taxonomy (Venanus and one species of Apanteles). Morphologial terms follow those of Huber and Sharkey (1993), and Sharkey and Wharton (1997), with some additional measurements following Mason (1981) and Valerio et al. (2009). When providing measurements, the first figure is that of the holotype, followed by the range for the rest of the specimens if different. For the holotypes a detailed transcription of all labels is provided. All types are deposited in the CNC.

Whenever possible, DNA barcoding (henceforth referred as "barcoding") data for the new species were added to the descriptions. DNA extraction, PCR and sequencing were done at the Canadian Centre for DNA Barcoding (University of Guelph, ON). DNA extracts were prepared from small pieces of legs using a glass fibre protocol. Extracts were resuspended in $30 \mu \mathrm{l}$ of $\mathrm{dH}_{2} \mathrm{O}$, and a 658 -bp region near the 5 ' terminus
of the COI gene was amplified using primers (LepF1-LepR1) following standard protocols (Ivanova et al. 2006). Composite sequences or CO1 fragments smaller than the barcode standard were generated using internal primers when initial amplification was not successful. Sequence divergences were calculated using the K2P distance model (Kimura 1980) and a NJ tree of distances was generated using the MEGA software (Tamura et al. 2007) to provide a graphic representation of the species divergences. Full details of methodology are as in Smith et al. (2008).

For barcoded specimens, the Supplementary Appendices 1-3 show their Sample ID and Process ID from BOLD (Barcoding of Life Data systems, www.barcodinglife. org). Sample IDs allow retrieval of all information associated with a particular specimen from the BOLD database, while Process IDs provide information about the sequence, trace files, laboratory processing, etc. Genbank accession numbers for the type material correspond to records HQ200902-HQ200929.

All genera, and species within each genus, are ordered alphabetically in the annotated checklist. General comments about species diversity, both reported here and estimated, availability of taxonomical reviews, and specimens in collections are provided for every genus. A detailed distribution within Canadian provinces and territories is provided for every species; acronyms follow the Canada Post standard (http://www. canadapost.ca/tools/pg/manual/PGaddress-e.asp).

Distribution outside of Alaska/Canada, based on data from Yu et al. (2005), is also briefly mentioned, using the following acronyms: ENA, CNA and WNA (eastern, central and western North America), PAL (Palearctic), HOL (Holarctic), and NEO (Neotropical).

Biological information is provided only when new or relevant. No intent has been made here to comprehensively deal with the hosts of Microgastrinae in the region. More than 10,000 reared but unidentified specimens in the CNC are currently under study; those results, when available, will be published elsewhere.

It was not possible to establish the specific identity of 29 species (13\%) with certainty. They are recorded here only to genus followed by a number (e.g. Cotesia sp. 1) and information on the specimens examined is provided. In most cases, study of the Holarctic fauna will be needed before determining their status.

## Results and discussion

A total of 28 genera and at least 225 species are recorded for Canada and Alaska, representing a $50 \%$ increase in the number of known species (Table 1). The genera Distatrix, Iconella, Protomicroplitis and Pseudapanteles for Canada, and Diolcogaster for Alaska are recorded for the first time. Except for Iconella and Protomicroplitis, these records also represent the northernmost extension of their known distribution.

Although the increase in species numbers is significant, many gaps still remain in our understanding of the group in Canada/Alaska. For example, the list of species for the northern areas (AK, NT, NU and YT), the Atlantic provinces and the Prairies are far

Table I. Number of species of Microgastrinae in Alaska, Canadian provinces and territories. (I) Number of species previously recorded based on Yu et al. (2005) and Fernández-Triana et al. (2009b). (2) Number of species recorded in the present paper. (3) Increase in the species number (\%).

|  | AB | AK | BC | MB | NB | NL | NS | NT | NU | ON | PE | QC | SK | YT | ALL |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| $(1)$ | 25 | 13 | 45 | 10 | 26 | 9 | 22 | 6 | 1 | 80 | 3 | 47 | 8 | 1 | 151 |
| $(2)$ | 38 | 16 | 73 | 57 | 46 | 20 | 38 | 10 | 4 | 136 | 8 | 97 | 16 | 3 | 225 |
| $(3)$ | 52 | 23 | 62 | 470 | 77 | 112 | 73 | 67 | 300 | 70 | 167 | 106 | 100 | 200 | 50 |

from complete; and studies currently underway should increase significantly the numbers provided in this paper. Similarly, the examination of specimens housed in western Canadian collections will be necessary if progress is to be made in $B C, A B$ and $S K$.

Based on this paper and work in progress, the latitudinal gradient of species and genera richness within the studied area show a marked increase towards south (Fig. 1), as would be expected. North of $80^{\circ} \mathrm{N}$ (northern tip of Ellesmere Island) there are only $4-5$ species in 3 genera of Microgastrinae. Between $70-80^{\circ} \mathrm{N}$ (most of the Canadian Arctic Archipelago with a few areas from the mainland, comprising almost exclusively tundra) there are $20-25$ species from about 5 genera. Within the latitudinal range of $60-70^{\circ} \mathrm{N}$ (most of Alaska and the three Canadian territories, comprising mostly boreal forest with some tundra) there are at least 150 species and 15 genera (e.g. Fernández-Triana et al. 2009a). The southernmost range considered here ( $45-60^{\circ} \mathrm{N}$, comprising the rest of Canada with many ecoregions represented) has over 250 species in 26 genera, but these figures are less conclusive because many more species await to be recorded -and thus should be seen as an underestimate.

The biogeographical affinities of the fauna can be analyzed from the distributional data detailed in the checklist below. If only the described species (197 in total) are accounted for, $67 \%$ are widely distributed in the Nearctic, especially in Eastern North America (the latter could be an artefact due to the more intensive studies and efforts done in that area); $15 \%$ are Holarctic species, many of them intentionally introduced for Biological Control programs; 10\% are strict Canada/Alaska endemics (which is equivalent to say that they are restricted to the northern part of the Nearctic region); $4 \%$ of the species are also found in the Neotropics; and $4 \%$ are cosmopolitan.

The most diverse genera are Cotesia, Apanteles, Microplitis, Pholetesor and Dolichogenidea, while Microgaster, Glyptapanteles and Diolcogaster also have significant, though smaller, number of species. Of these, only Pholetesor has been recently revised (Whitfield 2006) and its figure should be close to the actual number of species expected in the region (but see the checklist below). For the other genera (and especially for Cotesia, Microplitis, Apanteles, Dolichogenidea and Glyptapanteles), the figures provided here represent just a fraction of the actual diversity; with many more undescribed species among the CNC holdings as well as some that have been recently listed (e.g. Fernández-Triana et al. 2009b). These records are not considered in this paper because comprehensive taxonomic reviews are needed to unravel the true magnitude of Microgastrinae in the region, a daunting task that will require years of work.


Figure I. Latitudinal gradients in the species and genera richness of Microgastrinae from Canada and Alaska. Figures based on this paper and work in progress.


Figure 2. Localities of specimens (A), and cumulative number of species (B), of Microgastrinae from Canada and Alaska sampled for DNA barcoding. Based on data from BOLD (see Methods for more details).

It is difficult to provide accurate estimates of the actual diversity of the subfamily when so many species await study. However; the analysis of the available DNA barcoding data, the revision of the collections made so far, and the information of well studied areas (see below) suggest that the actual diversity of Microgastrinae in Alaska/Canada will be at least twice the number recorded in the present paper.

Table 2. Number of Lepidoptera and Microgastrinae species in selected areas of Canada. The figures are rounded to the nearest tenth for Microgastrinae species and to the nearest integer for the $\mathrm{L} / \mathrm{M}$ ratio. For Lepidoptera the data are taken from Danks (1981) for the Arctic Archipelago; Lafontaine and Wood (1997) for the Yukon; and Lafontaine (1997) for Ottawa. Microgastrinae figures are based on the present paper and unpublished data of the author.

| Area | Latitude (Area in $\mathbf{k m}^{2}$ ) | \# Lepidoptera (L) | \# Microgastrinae (M) | L/M Proportion |
| :---: | :---: | :---: | :---: | :---: |
| Canadian Arctic Archipelago | $\begin{aligned} & >70^{\circ} \mathrm{N} \\ & \left(1,400,000 \mathrm{~km}^{2}\right) \end{aligned}$ | 136 | 20 | 7 |
| Yukon Territory | $\begin{aligned} & 60-70^{\circ} \mathrm{N} \\ & \left(475,000 \mathrm{~km}^{2}\right) \end{aligned}$ | -2,000 | 120-150 | 13-17 |
| Ottawa and surroundings | $\begin{aligned} & 45^{\circ} \mathrm{N} \\ & \left(-8,000 \mathrm{~km}^{2}\right) \end{aligned}$ | 2,068 | 150-200 | 10-14 |

There are currently over 3,500 specimens of microgastrine wasps in BOLD with CO1 sequences, collected from localities all over Canada and Alaska (Fig. 2A). In spite of the relatively small proportion of specimens barcoded (compared to the more than 30,000 specimens from Canada and Alaska available in the collections studied) they represent over 240 species (Fig. 2B), an astonishing figure that surpasses the total of species listed in the present paper. DNA barcoding has proven to be a reliable tool to separate species of Microgastrinae (e.g. Smith et al. 2008), especially when supplemented by critical natural history data, and has tremendous potential to help reveal cryptic species for such a diverse subfamily.

The proportion of Lepidoptera to Microgastrinae from three well known areas within the region was also calculated (Table 2) and then the average was extrapolated to estimate the total of Microgastrinae for Alaska/Canada. Choosing Lepidoptera makes sense because they are a much better known group and, most importantly, they are the hosts of Microgastrinae, which parasitizes almost all of the lepidopteran families (Whitfield 1997). The proportion of host/parasitoid species was between 7 and 17 , with an average of 12 . Interestingly, the same proportion (10-12) is found in other well studied areas around the world such as temperate British Isles and tropical Area de Conservacion de Guanacaste, Costa Rica - data calculated from Fauna Europaea (van Achterberg 2004) and Janzen et al. (2009) respectively. If a proportion of 12 Lepidoptera to each Microgastrinae is extrapolated to the all Canada/Alaska fauna -with over 6700 estimated species of Lepidoptera (Biological Survey of Canada 2010), the results show an estimated diversity of about 550 species of Microgastrinae for the region.

Regardless of the approach used, even the most conservative scenarios show an unexpected and unprecedented level of species diversity in a region of the planet supposed to have a rather low diversity. The results reported here, as well as previous papers from other areas (e.g. Smith et al. 2008) suggest that indeed the Microgastrinae might be much more diverse than anticipated.

## Description of new species

## Apanteles huberi Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:D245A5D6-6061-46B0-A0FA-9271F0DB82DE
Figs 3, 6; Supplementary Appendix 1
Apanteles sp. 2. Fernández-Triana and Huber, 2010: 316. [Examined].

Type locality. Canada, British Columbia, Kispiox, $55^{\circ} 21^{\prime} 0$ " N, $127^{\circ} 40^{\prime} 58.8^{\prime \prime} \mathrm{W}$.
Type material. Holotype. Female (CNC), with first label: Choristoneura biennis, Kispiox, BC, T. G. Gray; second label with date as follows: 6.vii.1983; third label with Specimen ID: MIC 000108. CNC TYPE 23935.

Paratypes (CNC): $8+$ and $2 \delta^{\lambda}$ same data as holotype for the first two labels; 4 of those specimens with a third label with Specimen IDs: MIC 000106 and MIC 000107 (2 ) , MIC 000109 ( 1 §), and CNCI JDR-specm 2009-470 (1 $q$ ).

Diagnosis. This species will run to $A$. fumiferanae in both the keys of Muesebeck (1922) and Mason (1974); and will run to Apanteles sp. 2 in the key of FernándezTriana and Huber (2010). It is related to and morphologically very similar to A. fumiferanae. It differs in the propodeal areola shape (elongated coffin-shaped or ovoid, and weakly defined anteriorly in $A$. huberi; less elongated and well defined diamond-shaped in A. fumiferanae), length of flagellomeres 2 and 14 (longer in $A$. huberi) and medio tergite 1 (in $A$. huberi almost parallel-sided, with greatest width $1.1 \times$ the shortest width; while in $A$. fumiferanae the medio tergite is widening apically, with the greatest width $1.2-1.5 \times$ the shortest width). The two species also have different host species and differ in 1-4 base pairs within the barcoding region (more details below under the sections Molecular data, Distribution and biology and Comments).

Description. Female. Antenna length $2-2.2 \mathrm{~mm}$ (missing in holotype), body length $2.7 \mathrm{~mm}(2.3-2.8 \mathrm{~mm})$, forewing $2.8 \mathrm{~mm}(2.6-3.0 \mathrm{~mm})$. Head with glossa truncate and short. Face with shallow, sparse punctures; and sparse, uniformly distributed setae. Face width at antennal base/face width at clypeus edge: $1.1 \times$; intertentorial pit distance/face width at clypeus edge: $0.6 \times$; compound eye height/head height: $0.8 \times$; head height/width: $0.8 \times$; face width at antennal base/head maximum width: $0.7 \times$; malar space/basal width of mandible $1.1 \times$. Clypeus transversely narrow, its width/height: $3.7 \times$. Length/width of flagellomeres: 1st (3.5x), 2nd (4.0x), 8th (2.9×), 14th (1.2x), 15th $(1.1 \times)$. Length of flagellomere 2/flagellomere 14: $3.0 \times$. Ocello-ocular distance/ posterior ocelli diameter: $2.3 \times$; distance betwen posterior ocelli/ocelli diameter: $2.3 \times$.

Mesosoma. Pronotum laterally with dorsal and ventral grooves well defined. Mesoscutum with sparse and shallow punctures (distance between punctures about $1.0 \times$ its diameter), punctures sparser centrally. Mesoscutum $1.4 \times$ wider than long. Mesoscutum and scutellum uniformly covered by dense, silvered-coloured pilosity. Scutellum almost smooth, with very sparse and shallow punctures. Scutellum length/width at base $1.1 \times$. Scutellar suture thin and shallow, with $12-14$ costulae. Posterior band of


Apanteles huberi


## Apantles roughleyi

Figures 3-5. 3 Apanteles huberi, mesosoma, propodeum and medio tergites 1-3, dorsal 4 A. jenniferae, propodeum and medio tergites $1-3$, dorsal $\mathbf{5} A$. roughleyi, propodeum and medio tergites $1-3$, dorsal.


Figures 6-8. Wings. $\mathbf{6}$ Apanteles huberi $\mathbf{7} A$. jenniferae $\mathbf{8} A$. roughleyi. Scale line $=1.0 \mathrm{~mm}$.
scutellum polished. Scutellar lateral face with polished area semicircular and about 1/2 the face height. Mesopleuron setose and with punctures on the anterior margin and upper corner, rest smooth and glabrous; centrally with small depressed area with shallow transverse striae. Thin, crenulate sulcus separating meso and metapleura. Metapleuron mostly smooth and polished, with setae and punctures only dorsally and ventrally along margins; metapleuron with a short, crenulate, longitudinal sulcus running from lower margin near metacoxa through spiracle. Metapleural carina with a short lamella. Propodeum with an ovoid or coffin-shaped areola, with anterior carinae less defined; propodeum sparsely punctured in the anterior half, with transverse striation in the apical half.

Metasoma. Mediotergite 1 almost parallel sided, just slightly widening posteriorly; basal width/apical width $1.1 \times$; length/apical width $1.4 \times$; mediotergite 1 with smooth, basal depression; apical $2 / 3$ sculptured with longitudinal striae, except for a median, sub-apical depressed area which is mostly smooth and a polished knob centrally in the apical margin. Mediotergite 2 transverse, trapezoidal in shape; basal width/apical width $0.7 \times$; length/apical width $0.3 \times$; with longitudinal striae covering most of the surface. Mediotergite 3 twice the length of mediotergite 2 . Mediotergite 3 and following unsculptured, polished and uniformly covered by sparse setae. Hypopygium striate, with acute tip slightly protruding beyond apical tergites. Ovipositor sheaths fully setose, $0.9-1.0 \times$ as long as metatibia length.

Legs. Metatibial inner spur $1.3 \times(1.2-1.5 \times)$ the length of outer spur, and $0.6 \times$ $(0.5-0.6 \times$ ) the length of metatarsomere 1 . Metafemur $3.0 \times(3.0-3.1 \times)$ as long as wide.

Wings. Forewing vein R1a $1.1 \times$ as long as stigma length; length of R1a about $2.0 \times$ as long as the distance between its end and the end of $3 R S b$. Vein $\mathrm{r} 0.8 \times$ the maximum width of stigma. Join of veins $r$ and 2RS angulated, sometimes with small knob at their junction; vein 2 M $1.0-1.1 \times$ as long as vein ( $R S+\mathrm{M}$ )b. Edge of vannal lobe of hindwing medially straight to slightly convex and with setae of uniform length which are shorter than those at base and apex of lobe.

Colour: Maxillary and labial palps, and two first pairs of legs (except for coxae), yellow; head, meso and metasoma, and all coxae dark-brown or black; apex of metatibia and part (sometimes most) of the metafemur and metatarsus orange-red or light brown. Most of veins light brown, stigma borders light brown, centrally pale.

Male. As females, except for slightly smaller size (2.3-2.4 mm), legs with brighter yellow coloration, and width of mediotergite 1 slightly less than in females.

Molecular data. Partial barcodes (144 bp) from the holotype and three paratypes of $A$. huberi were obtained and compared with two paratypes of $A$. fumiferanae with a similar sequence length (Fig. 21). In spite of the relatively short sequences available for analysis (about one fifth of the barcoding region) the two species consistently differed between $1-4$ base pairs ( $0.8-2.8 \%$ ).

Distribution and biology. Only known from the type locality in BC. All studied specimens were reared from Choristoneura biennis -it is the only braconid species reliably reared from that lepidopteran (Fernández-Triana and Huber 2010).

Comments. The related species $A$. fumiferanae has a relatively wide range of hosts (Mason 1974; Fernández-Triana and Huber 2010), but has never been recorded parasitizing Choristoneura biennis. The different host species and slight but consistent morphological and barcoding differences provide sufficient evidence to consider $A$. huberi as a separate and distinct species.

Etymology. I dedicate this species to John Huber (CNC) as an appreciation for the many things I have learned from him during the last four years (his knowledge of Hymenoptera and kindness are both extraordinary); and also for all the shared chocolate!

## Apanteles jenniferae Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:B57489C7-8EC6-4513-A918-0844DF48BF45
Figs 4, 7
Apanteles sp. 1. Fernández-Triana and Huber, 2010: 316. [Examined].

Type locality. Canada, New Brunswick, Canterbury, $45^{\circ} 53^{\prime} 20.5^{\prime \prime} \mathrm{N}, 67^{\circ} 27^{\prime} 49.6^{\prime \prime W}$.
Type material. Holotype. Female (CNC), with first label as follows: C-26, Ex Choristoneura rosaceana Harr. on Red Maple; second label: Canterbury, York Co., N.B., 6.vii.1973. CNC TYPE 23936.

Paratypes (CNC): 3 Q , $2 \circlearrowleft^{\lambda}$ from Canterbury, NB; Galetta, Delta, and North Bay, ON; Old Chelsea and Tenoga, QC; ex: Choristoneura rosaceana (CNC).

Diagnosis. This species is related to $A$. fumiferanae but it is differentiated by its slightly larger size; yellow tegula; less defined areola (mostly marked by a depression and with only apical carinae; contrasting with a complete areola, well defined by carinae in $A$. fumiferanae); medio tergite 2 (less transverse in $A$. jenniferae, thinner in $A$. fumiferanae); and meditergite 3 (A. jenniferae with some sculpture centrally in anterior margin basally, completely smooth in $A$. fumiferanae).

Description. Female. Antenna length $2.2-2.3 \mathrm{~mm}$, body length 3.1 mm (3.0-3.4 $\mathrm{mm})$, forewing $3.2 \mathrm{~mm}(3.2-3.6 \mathrm{~mm})$. Head with glossa truncate and short. Face with shallow punctures (separation between punctures about the same than punctures diameter); and sparse, uniformly distributed setae. Face width at antennal base/face width at clypeus edge: $1.6 \times$; intertentorial pit distance/face width at clypeus edge: $0.6 \times$; compound eye height/head height: $0.7 \times$; head height/width: $0.8 \times$; face width at antennal base/head maximum width: $0.5 \times$; malar space/basal width of mandible $1.3 \times$.

Clypeus transversely narrow, its width/height: $3.5 \times$. Length/width of flagellomeres: 1 st $(3.9 \times)$, 2nd $(3.8 \times)$, 8th ( $3.0 \times$ ), 14th ( $1.4 \times$ ), 15 th ( $1.2 \times$ ). Length of flagellomere 2 / flagellomere 14: $2.6 \times$. Ocelo-ocular distance/posterior ocelli diameter: $2.0 \times$; distance betwen posterior ocelli/ocelli diameter: $2.0 \times$.

Mesosoma. Pronotum laterally with dorsal and ventral grooves well defined. Mesoscutum with relatively close punctures (distance between punctures about $0.5 \times$ its diameter). Mesoscutum $1.4 \times$ wider than long. Mesoscutum and scutellum uniformly covered by dense, silvered-coloured pilosity. Scutellum almost smooth, with very sparse and shallow punctures mostly on the margins. Scutellum length/width at base $1.0 \times$. Scutellar suture well impressed, with 12 costulae, the central ones more spaced and deeply impressed than the lateral ones. Posterior band of scutellum polished. Scutellar lateral face with polished area semicircular slightly less than half the face height. Mesopleuron setose and with punctures on the anterior half; the posterior half glabrous and smooth except for a thin sulcus running from the posterior margin (at about half the length of that margin) towards the lower margin of mesopleuron (ending just before the punctures and setae of the anterior half). Thin, crenulated sulcus separating meso and metapleura. Metapleuron mostly smooth and polished, with setae and punctures only dorsally and ventrally along margins; metapleuron with a very short, crenulate, longitudinal sulcus running from lower margin near metacoxa through spiracle. Metapleural carina with short lamella. Propodeum with areola defined mostly by a central impression than carinae -though the posterior carinae are visible; propodeum coarsely punctured in the anterior half, with transverse striation in the apical half, the only smooth area is centrally inside the areola.

Metasoma. Mediotergite 1 barrel-shaped, wider medially than anteriorly or posteriorly; basal width/apical width $0.9 \times(0.8-0.9 \times)$; length/apical width $1.1 \times$; mediotergite 1 with smooth, basal depression; apical $2 / 3$ coarsely sculptured and with longitudinal striae, except for a median, sub-apical depressed area which is mostly smooth and a polished knob centrally in the apical margin. Mediotergite 2 transverse, trapezoidal to almost rectangular in shape; basal width/apical width $0.7 \times$; length/apical width $0.3 \times$; coarsely sculptured with longitudinal and transverse striae covering most of the surface, the posterior margin bordered by distinct, crenulated punctures. Mediotergite 3 about $1.5 \times$ the length of mediotergite 2 and with some sculpture centrally in the anterior margin. Mediotergite 4 and following unsculptured, polished and uniformly covered by sparse setae. Hypopygium striate, with acute tip slightly protruding beyond apical tergites. Ovipositor sheaths fully setose, $1.0 \times(0.9-1.1 \times)$ as long as metatibia length.

Legs. Metatibial inner spur $1.4 \times(1.4-1.6 \times)$ the length of outer spur, and $0.6 \times$ $(0.5-0.6 \times$ ) the length of metatarsomere 1 . Metafemur $3.0 \times(3.0-3.2 \times)$ as long as wide.

Wings. Forewing vein R1a 1.0-1.1× as long as stigma length; length of R1a 6-7.0× as long as the distance between its end and the end of 3 RSb. Vein $r 1.0 \times(1.0-1.1 \times)$ the maximum width of stigma. Join of veins $r$ and 2RS angulated and with a small knob at their junction; vein $2 \mathrm{M} 0.8 \times(0.7-0.9 \times)$ as long as vein $(R S+M)$ b. Edge of vannal lobe of hindwing medially straight to convex and glabrous.

Colour: Maxillary and labial palps, tegula, two first pairs of legs (except for coxae), and basal half of metafemur yellow; head, meso and metasoma dark-brown or black; wing base and all coxae brown; metafemur, apical half of metatibia and metatarsus yellowish- brown to orange-brown. Most of veins very light brown, almost hyaline; stigma light brown.

Male. As female except for longer flagellomere, antenna longer than body length, darker hind legs (with metafemur dark brown), and less transverse medio tergite 2 (which is almost quadrate and with striation arranged in a concentric way).

Distribution and biology. The species is widely distributed in eastern Canada, where it has been reared from Choristoneura rosaceana.

Comments. This species and the previous one (A. huberi) illustrate well the need for a review of what Fernández-Triana and Huber (2010) called "the A. fumiferanae species-complex". It is becoming obvious that many species are hidden under that name, and a comprehensive approach combining detailed morphology, biology (especially verified host records) and molecular data will be required to unravel the rest of the species within that complex.

Etymology. I dedicate this species to Jennifer Read (CNC) to thank her for the many hours she spent taking photos for several projects we worked upon together; and as recognition for her superb photographic and editing skills.

## Apanteles masmithi Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:28705735-DE76-4BDD-AC43-65DF217462F2
Figs 13, 14; Supplementary Appendix 1
Type locality. Canada, Ontario, London, $42^{\circ} 59^{\prime} 1.32^{\prime \prime} \mathrm{N}, 81^{\circ} 14^{\prime} 58.92^{\prime \prime W} \mathrm{~W}$.
Type material. Holotype. Female (CNC), with first label as follows: London, ON, 23.viii.1953, W.W. Judd, on Typha heads; second label (yellow) with a code: 54-B-4; third label with a provisional identification by Mason (1955); fourth label with Specimen ID: MIC 000048. CNC TYPE 23937.

Paratypes (CNC): 3 \#F from London, ON, 23.viii.1953, W.W. Judd, on Typha heads, one of those specimens with a third label with Specimen IDs: MIC 000049; 5 \#F, 6 \#M from Digby, NS, 28.viii.1959, P.H.H. Gray, ex Limnaecia phragmitella, four of those specimens with a third label with Specimen IDs: MIC 000050, MIC 000051, MIC 000052 (3 \#F), and MIC 000054 (1 \#M); 5 \#F, 1 \#M from Lunenburg, NS, vi-vii. 1969, B. Wright, ex Gelechidae larvae on cat-tail heads, two of those specimens with a third label with Specimen IDs: MIC 000053 (1 \#F), and MIC 000057 (1 \#M); 2 \#F, 4 \#M, Brighton, NS, P.H.H. Gray, ex. Limnaecia phragmitella and Dycimotomia julianalis, on Typha heads, two of those specimens with a third label with Specimen IDs: MIC 000055 and MIC 000056 ( 2 \#M); $10^{\lambda}$, Leeds-Granville Co., forest, ixx.2008, S. B. Peck. Specimen ID: CAM 0456.

Diagnosis. This species looks similar to Apanteles cockerelli Muesebeck, 1921; and it will run to that species in the available keys (e.g. Muesebeck 1921). It differs in the
stigma colour in the fore wing (pale with only brown borders in $A$. masmithi, completely brown in $A$. cockerelli); the shape of vannal lobe in the hind wing (straight and with short setae medially in $A$. masmithi, concave and glabrous in $A$. cockerelli), and the relative length of the metatibial spurs (about the same length in $A$. masmithi, the inner spur longer than the outer one in $A$. cockerelli). The two species also have different geographic distribution, different host species, and differ in 14 base pairs within the barcoding region (more details below under the sections Molecular data, Distribution and biology and Comments).

Description. Female. Antenna length $2.6 \mathrm{~mm}(2.1-2.5 \mathrm{~mm})$, body length 3.7 mm (2.8-3.6 mm), forewing $3.5 \mathrm{~mm}(2.6-3.5 \mathrm{~mm})$. Head with glossa bilobated and rather long. Face smooth, with very shallow punctures (separation between punctures larger than punctures diameter) and very sparse setae. Face width at antennal base/face width at clypeus edge: $1.1 \times$; intertentorial pit distance/face width at clypeus edge: $0.6 \times$; compound eye height/head height: $0.7 \times(0.6-0.7 \times)$; head height/width: $0.9 \times$; face width at antennal base/head maximum width: $0.6 x$; malar space/basal width of mandible $1.7 \times$ (1.3-1.7x). Clypeus not much transverse, its width/height: $2.6 \times$. Length/width of flagellomeres: 1st $(3.1 \times), 2$ nd $(3.1 \times), 8$ th $(2.3 \times), 14$ th $(1.3 \times), 15$ th $(1.0 \times)$. Length of flagellomere 2/flagellomere 14: 2.2x. Ocelo-ocular distance/posterior ocelli diameter: $2.3 \times$ (1.9-2.3x); distance betwen posterior ocelli/ocelli diameter: $2.7 \times(2.1-2.7 \times)$.

Mesosoma. Pronotum very smooth and polished, laterally with dorsal and ventral grooves thin but deep and well defined. Mesoscutum mostly smooth, with shallow punctures (distance between punctures about its diameter), punctures a little closer and deeper in the posterior margin. Mesoscutum $1.2 \times(1.1-1.2 \times)$ wider than long. Mesoscutum and scutellum covered by sparse, silvered-coloured pilosity. Scutellum almost smooth, with very sparse (distance between punctures twice its diameter) and shallow punctures concentrated mostly on the margins. Scutellum length/width at base $1.1 \times$. Scutellar suture thin and shallow, with $16(15-17)$ costulae. Posterior band of scutellum polished. Scutellar lateral face with the polished area triangular and about $4 / 5$ the face height. Mesopleuron smooth and glabrous on most of its surface, with sparse setae and punctures (distance between punctures twice or more its diameter) only on the anterior and dorsal margins. Thin and shallow sulcus, with a few costulae, separating meso and metapleura. Metapleuron mostly smooth and polished, with setae and sparse punctures only dorsally and posteriorly along margins; metapleuron with a thin, longitudinal sulcus running from lower margin through spiracle. Metapleural carina with short lamella. Propodeum mostly smooth, with sparsely punctures in the anterior half and a few transverse striae in the apical half; propodeal areola absent but there is a short, postero-median longitudinal band of rugosity (consisting of several very short carinae radiating from nucha).

Metasoma. Mediotergite 1 arched and strongly narrowing toward apex, with a wide and deep basal depression; basal width/apical width $2.2 \times$; length/apical width $2.3(2.0-2.3 \times)$; mediotergite 1 mostly smooth, polished and glabrous, with a few setae and elongated, longitudinal punctures postero-laterally. Mediotergite 2 smooth and polished, transverse, and wider centrally; basal width/apical width $1.0 \times(0.9-1.0 \times)$;
length/apical width $0.5 \times(0.3-0.5 \times)$. Mediotergite $32.0 \times(2.0-2.5 \times)$ the length of mediotergite 2. Mediotergite 3 and following unsculptured, polished and uniformly covered by setae. Hypopygium striate, with acute tip protruding beyond apical tergites. Ovipositor sheaths fully setose, $1.9 \times(1.8-1.9 \times)$ as long as metatibia length.

Legs. Metatibial inner spur about the same length of outer spur, and $0.4 \times(0.4-$ $0.5 \times$ ) the length of metatarsomere 1 . Metafemur $2.8 \times$ as long as wide.

Wings. Forewing vein R1a $1.0 \times$ as long as stigma length; length of R1a $5.0 \times$ as long as the distance between its end and the end of 3 RSb . Vein $\mathrm{r} 0.8 \times$ the maximum width of stigma. Join of veins $r$ and $2 R S$ angulated and with a small know marking the angulation (sometimes only slightly angulated and then know very small to absent); vein $2 \mathrm{M} 0.6 \times$ as long as vein $(\mathrm{RS}+\mathrm{M})$ b. Edge of vannal lobe of hindwing medially straight and with short setae that are slightly sparser than the rest of the lobe.

Colour: Mostly black to dark brown, except for: maxillary and labial palps (light brown to brown), wing base (light brown), profemur and part of most of all tibia and tarsi (light brown to yellow), meso and metatibial spurs (light yellow to witish). Wings hyaline, with most of veins transparent, except for $\mathrm{C}+\mathrm{Sc}+\mathrm{R}, \mathrm{R} 1$, and occasionally r and 2RS which can be partially pigmented; stigma hyaline except for brownish borders.

Male. Similar to females but slightly smaller in size and with longer antennal segments (especially the apical ones). The maxillary and labial palpi tend to be yellow, and the legs tend to be darker (mostly black with less yellow areas). The mediotergite 1 is fully smooth and polished, and narrows stronger toward apex (being thinner compared to that of females). The wing veins are paler, of milky coloration, including the stigma (which brown borders are very thin, almost disappearing in some specimens).

Variation. There is some variation in size among the different localities (it is shown in the description) and also the maxillary and labial palpi range from dark brown to yellow.

Molecular data. Barcodes of 6 specimens of $A$. masmithi and 3 of the related species $A$. cockerelli were compared. Because all specimens but one were collected between 1951 and 1969 it was only possible to obtain mini-barcodes ( 144 bp ). The only recent specimen (a paratype of $A$. masmithi, collected in 2008) rendered a full barcode (657 bp ) which fully matched the other specimens with mini-barcodes. The molecular results confirmed that they are indeed different species, with at least 14 (9.7\%) of base pairs divergence (Fig. 22). Interestingly, specimens of $A$. cockerelli within the US (from CA, MO and TX) seem to comprise more than one species -but that is beyond the geographical scope of the present work, thus they will be dealt with in a different paper.

Distribution and biology. The species is widely distributed in Eastern Canada, where it has been recorded parasitizing Limnaecia phragmitella (Gelechidae) on Typha spp. heads (cattail grass). Some paratypes from Nova Scotia had written on their labels that the host could also be Dycimotomia julianalis (Pyralidae), also on cattail; however, this record needs to be confirmed. This is the first Microgastrinae (and Braconidae) species recorded as parasitoid of L. phragmitella.

Comments. The specimens of $A$. masmith $i$ were identified by W. Mason as a different but related species to $A$. cockerelli. The latter species has been recorded from

US in the following ten states: CA, IA, ID, MI, MO, NE, NM, OR, SD, TX (Yu et al. 2005). The different host species (Isophrictis sp. (Gelechidae) for $A$. cockerelli), 14 ( $9.7 \%$ ) of base pairs divergence within the barcoding region, and slight but consistent morphological differences, provide sufficient evidence to consider $A$. masmithi as a distinct species.

Etymology. I dedicate this species, which DNA barcoding helped to recognize, to M. Alex Smith (University of Guelph) as an appreciation for the many parasitoid wasps he has helped to barcode, study and publish about; and also for sharing with me his superb knowledge on molecular approaches.

## Apanteles roughleyi Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:E392BA33-CAC1-40F2-ADE5-440D4B017969
Figs 5, 8
Apanteles sp. near stagmatophorae. Fernández-Triana and Huber, 2010: 316. [Examined].

Type locality. Canada, British Columbia, Mill Bay, $48^{\circ} 39^{\prime} 2^{\prime \prime} \mathrm{N}, 123^{\circ} 33^{\prime} 33^{\prime \prime} \mathrm{W}$
Type material. Holotype. Female (CNC), with first label with Specimen ID: CNCI JDR-specm 2009-463; second label with Forest Insect Survey number: 65.21.01A, and date: $22.1 i i .1965$; third label as follows: A. grandis [probably Abies grandis], Mill Bay, B.C.; fourth label: Ex? Choristoneura fumiferanae; fifth label with a provisional identification by Mason 1978. CNC TYPE 23938.

Diagnosis. This species looks similar to A. stagmatophorae Gahan, 1919, and it will run to that species in the available keys (e.g. Muesebeck, 1921), but they differ in several characteristics. In $A$. roughleyi the vannal lobe of hindwing is medially straight and glabrous (slightly convex to slightly straight but with uniform setae in A. stagmatophorae), the ovipositor sheaths are longer ( $1.7 \times$ compared to $1.2 \times$ ), the metafemur is thinner ( $3.5 \times$ as long as wide compared to $3.2 \times$ ), and the propodeum is more sculptured (in A. stagmatophorae the propodeum is mostly smooth, with very shallow and small punctures). The two species have a very separate distribution (BC in western Nearctic for $A$. roughleyi; Maryland, in eastern Nearctic for $A$. stagmatophorae). The known host are also from different families: Choristoneura sp., Tortricidae, for $A$. roughleyi; Periploca gleditschiaeella (Chambers, 1876), Cosmopterigidae, for $A$. stagmatophorae (more details below in the section Distribution and biology).

Description. Female. Antenna broken, body length 3.3 mm , forewing 3.5 mm . Head with glossa truncate and short. Face with shallow punctures (separation between punctures about the same than punctures diameter) and uniformly distributed setae. Face width at antennal base/face width at clypeus edge: $1.0 \times$; intertentorial pit distance/face width at clypeus edge: $0.5 \times$; compound eye height/head height: $0.8 \times$; head height/width: $0.8 \times$; face width at antennal base/head maximum width: $0.7 \times$; malar space/basal width of mandible $1.2 \times$. Clypeus transversely narrow, its width/height:
$3.0 \times$. Length/width of flagellomeres: 1st (2.6x), 2nd (2.2×), 8th (2.3×), flagellomeres $12+$ missing. Ocelo-ocular distance/posterior ocelli diameter: $2.0 \times$; distance betwen posterior ocelli/ocelli diameter: $2.0 \times$.

Mesosoma. Pronotum laterally with dorsal and ventral grooves thin, but well defined and deep. Mesoscutum with very shallow and sparse punctures (distance between punctures $1.5-2.0 \times$ its diameter). Mesoscutum $1.4 \times$ wider than long. Mesoscutum uniformly covered by silvered-coloured pilosity; scutellum almost glabrous, with just a few setae on margins. Scutellum almost smooth, with very sparse, small and shallow punctures mostly on the center. Scutellum length/width at base $1.1 \times$. Scutellar suture very thin and shallow, with about 20 small and not well defined costulae. Posterior band of scutellum polished. Scutellar lateral face with polished area semicircular about $0.6 \times$ the face height. Mesopleuron setose and with sparse punctures only on the anterior margin; the rest glabrous, smooth and polished. Thin, crenulated sulcus separating meso and metapleura. Metapleuron mostly smooth and polished, with setae and punctures only dorsally and ventrally along posterior margin; metapleuron with a thin sulcus running from lower margin near metacoxa through spiracle. Metapleural carina with a very short lamella. Propodeum mostly punctured, with a few striae posterolaterally; propodeal areola absent, but there is a central smooth area (contrasting with rest of the propodeum sculpture) and also there is a short, postero-median longitudinal band of rugosity (consisting of several short carinae radiating from nucha).

Metasoma. Mediotergite 1 narrowing towards apex; basal width/apical width $1.6 \times$; length/apical width $1.9 \times$; mediotergite 1 with smooth, basal depression; apical half coarsely punctured, except for a polished knob centrally in the apical margin. Mediotergite 2 transverse, trapezoidal in shape; basal width/apical width $0.5 \times$; length/ apical width $0.2 \times$; sculptured with longitudinal striation and puntures covering most of the surface except the center. Mediotergite $31.6 \times$ the length of mediotergite 2 . Mediotergite 3 and following unsculptured, polished and uniformly covered by setae. Hypopygium striate, with an acute tip protruding well beyond the apical tergites. Ovipositor sheaths fully setose, $1.7 \times$ as long as metatibia length.

Legs. Metatibial inner spur $1.1 \times$ the length of outer spur, and $0.5 \times$ the length of metatarsomere 1 . Metafemur $3.5 \times$ as long as wide.

Wings. Forewing vein R1a $1.3 \times$ as long as stigma length; length of R1a $5.7 \times$ as long as the distance between its end and the end of 3 RSb . Vein r $1.0 \times$ the maximum width of stigma. Join of veins r and 2 RS slightly angulated; vein $2 \mathrm{M} 1.1 \times$ as long as vein (RS $+M)$ b. Edge of vannal lobe of hindwing medially straight and glabrous.

Colour: Mostly black to dark brown, except for: maxillary and labial palps (yellow); tegula and wing base (light brown); first two pairs of legs (yellow except for coxae which are partially light brown); hind legs (mostly yellow-brown, with metacoxa brown and dorsal brown marks on metafemur, metatibia and metatarsi). Wings hyaline, with most of veins brown, including stigma.

Male. Unknown.
Distribution and biology. The host information (Choristoneura fumiferana) was recorded originally in 1965, i.e., before Freeman (1967) split the genus Choristoneura
and changed the species boundaries. The actual host is either C. occidentalis or C. pinus, but there is no way to determine which.

Comments. The specimen bears a label by W. Mason, dated 1978, stating that it may actually be a new species related to $A$. stagmatophorae. Comparison with two paratypes of the later species (housed in the CNC) confirms that the two species are distinct. In spite of the fact there is only one known specimen, the species is described to provide a name because of its potential economic importance (Fernández-Triana and Huber 2010).

Etymology. I dedicate this species to the late Rob Rougley (University of Manitoba) who passed away when this paper was starting. We all miss you dear friend and colleague, but I am sure you should be chasing heavenly Ditiscidae beetles right now!

## Apanteles samarshalli Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:D62FD0A7-E529-4162-8233-49C471073C64
Figs 9-12; Supplementary Appendix 1

Type locality. United States, Florida, Monroe County, Key Largo, $25^{\circ} 5^{\prime} 11.4^{\prime \prime} \mathrm{N}$, $8^{\circ} 26^{\prime} 50.28^{\prime \prime} \mathrm{W}$.

Type material. Holotype. Female (CNC), with first label: FLA: Monroe Co., N. Key Largo, secondary hammock forest, iii-iv.1985; second label with Specimen ID: CNCH1234. CNC TYPE 23939.

Paratypes (CNC): 2 q from N. Key Largo, Monroe Co., FL, secondary hammock forest, iii-iv.1985; 2 Q from Fat Deer Key, Monroe Co., FL, iii-iv.1985; 1 q from Everglades National Park, Royal Palm Hammock, Monroe Co., FL, hammock forest, iii-iv.1985, S \& J. Peck; 2 \& from Archbold Biological Station, Highlands Co., FL, 26.iv.1967, B. V. Peterson; 1 from Rondeau Prov. Pk, ON, Mal. Trap, 19.viii-11. ix. 1973.

Diagnosis. Thus far this is the only Nearctic species of Apanteles with a significantly short antenna (half the body length); vein 2 M very short, almost obliterating with vein 2RS; and antenna with yellow scape/pedicel and brown flagellomere. The combination of those characters makes $A$. samarshalli one of the most distinctive and recognizable species within the genus.

Description. Female. Antenna length $1.3 \mathrm{~mm}(1.3-1.5 \mathrm{~mm}$ ), body length 2.6 $\mathrm{mm}(2.5-3.0 \mathrm{~mm})$, forewing $2.3 \mathrm{~mm}(2.3-2.5 \mathrm{~mm})$. Head with glossa truncate and short. Face with shallow punctures (separation between punctures about the same as its diameter). Face width at antennal base/face width at clypeus edge: $1.0 \times$; intertentorial pit distance/face width at clypeus edge: $0.5 \times$; compound eye height/ head height: $0.7 x$; head height/width: $0.8 \times$; face width at antennal base/head maximum width: $0.6 \times$; malar space/basal width of mandible $1.0 \times$. Clypeus transverse, its width/height: $3.0 \times$. Length/width of flagellomeres: 1st (1.6x), 2nd (1.4x), 8th $(0.8 x)$, 14th $(0.8 x), 15$ th $(0.9 x)$. Length of flagellomere 2/flagellomere 14: 1.9x.


Figures 9-12. Apanteles samarshalli. 9 Dorsolateral I0 Lateral II Ventral $\mathbf{I 2}$ Propodeum and medio tergites 1-2.

Ocelo-ocular distance/posterior ocelli diameter: $1.8 \times$; distance betwen posterior ocelli/ocelli diameter: 1.9×.

Mesosoma. Pronotum laterally with dorsal and ventral grooves well defined. Mesoscutum with coarse, close punctures (distance between punctures less than half its diameter). Mesoscutum $1.2 \times(1.1-1.2 \times)$ wider than long. Mesoscutum and scutellum covered by uniform, large, silvered-coloured pilosity. Scutellum almost smooth, with very shallow and sparse punctures in the margins. Scutellum length/width at base $0.8 \times$. Scutellar suture width $1 / 6$ scutellum length, with 12-14 costulae. Posterior band of scutellum polished. Scutellar lateral face with the polished area triangular and about $4 / 5$ the face height. Mesopleuron with close punctures and setae on the anterior half, smooth and glabrous on the posterior half. Thin and shallow sulcus, with fine costulae, separating meso and metapleura. Metapleuron mostly punctured and with setae, smooth, polished and glabrous only around the spiracle; metapleuron with a longitudinal sulcus running from ventral to dorsal margin of metapleuron through spiracle. Metapleural carina lamellate. Propodeum sculpture
reticulate, postero-laterally with longitudinal striation; propodeal areola absent but there is a short, postero-median longitudinal band of rugosity (consisting of several short carinae radiating from nucha).

Metasoma. Mediotergite 1 evenly and slightly narrowing toward apex, with a wide and deep basal depression; basal width/apical width $1.4 \times$; length/apical width 1.5 ; mediotergite 1 mostly sculptured (except for smooth basal depression and central knob on the posterior margin), with longitudinal striation on its apical $2 / 3$. Mediotergite 2 smooth and polished, transverse, and wider centrally; basal width/apical width $0.8 \times$; length/apical width $0.3 \times$. Mediotergite $32.0-2.5 \times$ the length of mediotergite 2 . Mediotergite 3 and following unsculptured, polished and covered by sparse setae on the posterior margins. Hypopygium striate, with acute tip slightly protruding beyond apical tergites. Ovipositor sheaths fully setose, short, $0.6 \times$ as long as metatibia length.

Legs. Metatibial inner spur $1.3 \times$ the length of outer spur, and $0.5 \times$ the length of metatarsomere 1. Metafemur $2.7 \times$ as long as wide.

Wings. Forewing vein R1a $1.3 \times(1.2-1.5 \times)$ as long as stigma length; length of R1a $4.0 \times(4.0-5.0 \times)$ as long as the distance between its end and the end of $3 R S b$. Vein $r$ about the same length than maximum width of stigma. Join of veins $r$ and 2RS evenly curved, not angulated; vein 2 M very short, almost obliterating with 2 RS , length of $2 \mathrm{M} 0.3 \times$ as long as vein $(\mathrm{RS}+\mathrm{M}) \mathrm{b}$. Edge of vannal lobe of hindwing medially strongly concave and glabrous.

Colour: Body black; antenna flagellomere, metacoxa, most of the metafemur and apical $1 / 4$ of metatibia brown; mandibles, labrum, maxillary and labial palps, scape, upper corner of pronotum, tegula and laterotergites $1-3$, yellow. Wings hyaline, with most of veins brown pigmented; stigma brown with a minute pale spot basally.

Male. Unknown.
Molecular data. From all specimens studied, only the holotype rendered a partial sequence ( 390 bp , approximately $60 \%$ of the barcoding region). The specimen matches almost perfectly (99.96\%) a Costa Rican species named as Apanteles Rodriguez151 (Smith et al. 2008).

Distribution and biology. The species has been found from the southwestern part of ON (Rondeau Provincial Park, $42^{\circ} \mathrm{N}$ ) to about $25^{\circ} \mathrm{N}$ in FL (Everglades National Park and Florida Keys). None is know of its host, but most of the specimens have been collected in hammock forests.

Comments. Despite the two widely separate areas of distribution (ON and FL), I have not been able to find any difference between the Canadian and US specimens; thus they are considered as conspecific here. As for the relation with Apanteles Rodriguez151, I have not been able to examine specimens of the latter. If proven conspecific, it would be even more puzzling to explain the distribution of the species. All of those areas share in common the presence of oaks, but the data available is not enough as to draw any solid conclusion at present.

Etymology. I dedicate this species to a great friend and entomologist, Steve A. Marshall (University of Guelph). I hope you have many more collecting and photography trips in the near future!

## Distatrix carolinae Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:85F029F2-74E5-4EE5-A041-02C9520A0E3B
Figs 15, 16
Type locality. Canada, Quebec, Gatineau, $45^{\circ} 29^{\prime} 16^{\prime \prime} \mathrm{N}, 75^{\circ} 51^{\prime} 52^{\prime \prime} \mathrm{W}$.
Type material. Holotype. Female (CNC), with label as follows: Summit King Mtn. Old Chelsea, QUE, 26.vi.77, M. Sandborne. CNC TYPE 23940.

Diagnosis. This species is very similar to D. solanae Whitfield, 1996, the other known Nearctic species. They differ slightly in body coloration (meso and metasoma mostly dark brown in $D$. carolinae, mostly honey-orange in $D$. solanae), length/width of flagellomere 2 and $14(2.9 \times$ and $3.3 \times$ for $D$. carolinae and $3.7 \times$ and $3.8 \times$ for $D$. solanae respectively) and a longer inner metatibial spur compared to the outer one ( $1.5 \times$ in $D$. carolinae, $1.2 \times$ in $D$. solanae). The raised medial region of mediotergite 2 is delimited by divergent grooves that fade posteriorly in $D$. solanae while the grooves are more or less parallel and not fading posteriorly in $D$. carolinae.

Description. Female. Antenna length 3.5 mm ; body length 3.2 mm ; forewing length 3.7 mm . Head with glossa truncate and short, maxillary and labial palps light yellow. Face with shallow and sparse punctures and uniformly distributed setae. Face width at antennal base/face width at clypeus edge: $1.1 \times$; intertentorial pit distance/face width at clypeus edge: $0.7 \times$; compound eye height/head height: $0.8 \times$; head height/ width: $0.8 \times$; face width at antennal base/head maximum width: $0.4 \times$; malar space/ basal width of mandible $1.3 \times$. Clypeus transversely narrow, its width/height: $4.6 \times$. Length/width of flagellomeres: $1^{\text {st }}(3.0 \times), 2^{\text {nd }}(2.9 \times), 3^{\text {rd }}(3.0 \times), 8^{\text {th }}(3.0 \times), 14^{\text {th }}(3.3 \times)$, $15^{\text {th }}(3.0 \times), 16^{\text {th }}(3.2 \times)$. Ocelo-ocular distance/posterior ocelli diameter: $0.4 \times$; distance betwen posterior ocelli/ocelli diameter: $0.8 \times$.

Mesosoma. Pronotum with ventral groove present, dorsal one almost obliterated. Mesoscutum with shallow, sparse punctures (distance between punctures about the same as its diameter); punctures almost disappearing in the notauli and posterior area of mesoscutum. Notauli not impressed, visible only because of the contrast of different coloration and smoother area than most of the mesoscutum. Mesoscutum $1.3 \times$ wider than long. Mesoscutum and scutellum uniformly covered by dense, silvered-coloured pilosity. Scutellum almost completely smooth. Scutellum length/width at base $1.2 \times$. Scutellar suture shallow and thin with $8-9$ costulae some of them confluent. Posterior band of scutellum polished. Scutellar lateral face with polished area about $1 / 3$ the face height. Mesopleura smooth and glabrous, except for a few punctures and setae on the margins; sternaulus marked by a shallow impression with transverse striae. Crenulated sulcus separating meso and metapleura. Metapleura smooth in basal half, apical half punctuated and with setae; metapleura with a crenulated, longitudinal sulcus running from lower margin near the metacoxa through the spiracle. Metapleural carina with lamella. Propodeum weakly punctuate, almost smooth; propodeal areola absent but there is a short, postero-median longitudinal band of rugosity (consisting of several short carinae radiating from nucha).


Figures I3-16. I3 Apanteles masmithi, lateral I4 A. masmithi, meso and metasoma, dorsal I5 Distatrix carolinae, lateral 16 D. carolinae, dorsal.

Metasoma. Mediotergite 1 parallel sided for over 3/4 of its length, then slightly narrowing towards apex where it is rounded at posterior end; basal width/apical width $1.8 \times$; length/apical width $3.6 \times$; mediotergite 1 essentially unscultured except postero-laterally near apical margin; with broad excavation medially over anterior half. Mediotergite 2 subtriangular but with lateral margins weakly defined; basal width/apical width $0.3 \times$; length/apical width $0.5 \times$; essentially smooth, with fine, longitudinal grooves sublaterally, delimiting a central, raised region that is more or less rectangular in shape. Mediotergite $31.2 \times$ longer than mediotergite 2. Mediotergite 3 and following unsculptured, polished and with sparse setae. Hypopygium evenly sclerotized, truncated and slightly longer than apical tergites. Ovipositor sheaths very short (visible part $1 / 10$ the length of metatibia), the tip blunt and with very sparse, tiny setae (those setae much shorter than hypopygium pilosity).

Legs. Metatibial inner spur $1.5 \times$ the length of outer spur, and $0.7 \times$ the length of metatarsomere 1. Metafemur $3.6 \times$ as long as wide. Protarsus with Protapanteles-like spine. Tarsal claws basally with a large lobe that extends more than half the claw length.

Wings. Fore wing vein R1a as long as stigma length; length of R1a about $5.0 \times$ as long as the distance between its end and the end of 3 RSb . Vein $\mathrm{r} 0.8 \times$ the maximum width of stigma. Vein $r$ meeting 2RS in a distinct angle marked by a knob. Vein 2M about the same length that vein $(R S+M) b$. Hindwing with margin of vannal lobe medially straight and without setae in the flat area.

Colour: Maxillary and labial palps, labrum, mandibles, scape, pedicel, tegula, wing base, all legs (except for metatibia apex which is darker), medio tergite 1 and most of sternite yellow. Flagellomere light brown; clypeus orange-brown. Mesosoma dark brown, except for most of propleura and pronotum, notauli, lateral margins and apical 1/4 of mesoscutum which are honey-orange. Head brownish-black. Rest of metasoma brown. Stigma and veins in forewing brown.

Distribution and biology. This species represents the northernmost record of the genus. Nothing is known of its biology.

Comments. Based on morphology only, the limits between $D$. carolinae and $D$. solanae seem weak; however, morphological similarities are common within this genus. For example: $D$. solanae shares a number of characteristics with Neotropical species (see Grinter et al. 2009). I consider the Canadian specimen as a new and distinct species based on the major differences within the localities and habitats (California's inner Coast Range and Oregon Cascade Mountains for D. solanae; King Mountain in Gatineau Park, Quebec, for $D$. carolinae). In the CNC there are several specimens representing at least another undescribed species from the Nearctic (southern and eastern US); the study of those specimen will clarify in time the limits of the North America species.

Etymology. I dedicate this species to Caroline Boudreault (CNC), who likes so much to ski and enjoy the Gatineau Park. Your friendship, advices and jokes are always a great encouragement!

## Pseudapanteles gouleti Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:35425DE9-DD0B-4118-8851-617694A01EFA
Figs 17-18; Supplementary Appendix 1

Type locality. Canada, Ontario, Ottawa, $45^{\circ} 21.365^{\prime} \mathrm{N}, 75^{\circ} 42.416^{\prime} \mathrm{W}$.
Type material. Holotype. Female (CNC), with labels as follows: CANADA: ON, Ottawa, $45^{\circ} 21.365^{\prime} \mathrm{N}, 75^{\circ} 42.416^{\prime} \mathrm{W}, 13-23 . v i i .2007, \mathrm{H}$. Goulet, malaise trap, city garden; second label with Specimen ID: CAM 0253. CNC TYPE 23941.

Paratypes (CNC): 1 q and $6 \delta$ same data than holotype except for collecting dates as follow: 13-23.vii. 2007 (2 © ), 30.vii-10.viii. 2007 (3 ठ) , 10.viii-1.ix. 2007 (1 Q, 1 ${ }^{\top}$ ) [Specimens ID: CAM 0251, 0252, 0254-0258]; 1 Q Quebec, Hull, Malaise Trap, 10.viii.1965; 5 ot Quebec, Hull, Malaise Trap, 31.viii.1965; 2 q Quebec, Old Chelsea, Summit King Mountain, 350 m, 22 and 27.viii.1965; 1 \& Ontario, Twp.


Figures I7-20. I7 Pseudapanteles gouleti, lateral 18 P. gouleti, mesosoma and mediotergites 1-3, dorsal 19 Venanus heberti, lateral 20 V . heberti, mesosoma and mediotergites 1-3 dorsal.

Nepean, 25. viii. 1949 , H. A. Tripp col., reared from an immature case of Paraclemensia acerifoliella collected 10.v.1949; 1 \& Ontario, St. Lawrence Islands National Park, McDonald Island, 5.viii.1976; 4 Ontario, St. Lawrence Islands National Park, Thwart-
 nisville, 6.viii.1963, W. R. Mason.

Diagnosis. Pseudapanteles gouleti is recognized by its more sculptured propodeum, with transverse carination all over its surface in addition to the median carina (the rest of the Nearctic species have the propodeum mostly smooth with only a median carina and at most a few, small transverse ridges radiating from base of median carina); the uniformly brown veins and stigma in the forewing (veins mostly hyaline and stigma hyaline centrally with margins light brown in the other species); mediotergite 1 fully sculptured, its basal 0.6 parallel-sided and then narrowing towards apex, its basal width about $1.2-1.3 \times$ its apical width (mediotergite 1 partially or fully smooth;
barrel-shaped in P. nigrovariatus and $P$. sesiae or strongly narrowing from base to apex in P. dignus).

Description. Female. Antenna length $2.2 \mathrm{~mm}(2.0-2.2 \mathrm{~mm})$, slightly shorter than body length ( 2.6 mm , range: $2.2-2.7 \mathrm{~mm}$ ) and forewing ( 2.7 mm , range: $2.3-2.7 \mathrm{~mm}$ ). Head with glossa bilobate and long. Face with shallow and sparse punctures and sparse, uniformly distributed setae. Face width at antennal base/face width at clypeus edge: $1.2 \times$; intertentorial pit distance/face width at clypeus edge: $0.5 \times$; compound eye height/ head height: $0.7 \times$; head height/width: $0.9 \times$; face width at antennal base/head maximum width: $0.6 \times$; malar space/basal width of mandible $1.1 \times$. Clypeus transversely narrow, its width/height: $4.5 \times$. Length/width of flagellomeres: 1st (2.3x), 2nd (2.7x), 3rd (2.3x), 8th $(2.0 \times), 14$ th $(1.0 \times), 15$ th $(1.0 \times), 16$ th $(1.0 \times)$. Ocelo-ocular distance/posterior ocelli diameter: $2.5 \times$; distance betwen posterior ocelli/ocelli diameter: $1.6 \times$.

Mesosoma. Pronotum XX. Mesoscutum uniformly sculptured by dense and well impressed punctures (distance between punctures about half their diameter). Mesoscutum $1.5 \times$ wider than long. Mesoscutum and scutellum uniformly covered by dense, silvered-coloured pilosity. Scutellum similarly sculptured than mesoscutum, though punctures slightly shallower and sparser. Scutellum length/width at base $1.2 \times$. Scutellar suture thin and shallow, with 8-9 costulae. Posterior band of scutellum polished. Scutellar lateral face with polished area about $1 / 2$ the face height. Except for a few punctures on the upper anterior margin, mesopleuron smooth and glabrous, setae over all of mesopleuron margins. Crenulated sulcus separating meso and metapleura. Metapleuron smooth in basal half, apical half punctate and with setae, metapleuron with a crenulated, longitudinal sulcus running from lower margin near metacoxa through spiracle. Metapleural carina with short lamella. Propodeum with median carina well defined and raised over its entire length; propodeum fully sculptured with transverse carinae, some radiating from the median carina.

Metasoma. Mediotergite 1 parallel sided for the basal $0.6 \times$ of its length, then narrowing towards apex, basal width/apical width $1.3 \times(1.2-1.3 \times)$; length/apical width $3.1 \times$; mediotergite 1 with deep medial groove over its basal half, fully sculptured with longitudinal to transverse striae (except for a very small basal area surrounding the beginning of the groove and a small, polished apical knob). Mediotergite 2 transverse, subtriangular to trapezoidal in shape; basal width/apical width $0.4 \times$; length/ apical width $0.4 \times$; fine, longitudinal striae covering most of the surface (sometimes apical third smooth). Mediotergite 3 more than twice the length of mediotergite 2. Mediotergite 3 and following unsculptured, polished and uniformly covered by sparse setae. Hypopygium striate, with acute tip protruding beyond apical tergites. Ovipositor sheaths fully setose, $1.0-1.2 \times$ as long as metatibia length.

Legs. Metatibial inner spur $1.4 \times$ the length of outer spur, and $0.47 \times$ the length of metatarsomere 1. Metafemur 3.2-3.5 $\times$ as long as wide.

Wings. Vein R1a $1.2-1.3 \times$ as long as stigma length. Length of R1a about $6.0 \times$ as long as the distance between its end and the end of 3 RSb . Vein $\mathrm{r} X$ the maximum width of stigma. Vein $r$ and 2RS evenly curved to very slightly arched, with no clear limits between the two veins. Vein 2 M about twice as long as vein (RS+M)b. Edge of
vannal lobe of hindwing medially straight to slightly convex and with uniform length setae shorter than those at base and apex of lobe.

Colour: Labrum, mandibles (except for black tips), scape and pedicel yellow; maxillary and labial palps light yellow; clypeus orange-brown; rest of antenna and head brown. Mesosoma, basal half of metacoxa and mediotergite 1 dark brown to black; mediotergite 2 completely, mediotergite 3 and following centrally, apical half of metacoxae dorsally, metatarsi and apex of metatibia, light brown; tegula, rest of legs, tergites 3 and following laterally, and all sterna, yellow to light yellow almost white; stigma and veins in forewing brown.

Male. Males have mediotergite 3 and following almost completely brown, clypeus, scape and pedicel darker, and metacoxa fully brown. The flagellomeres are longer than those of females.

Variation. Some specimens have lighter body coloration.
Molecular data. Eleven specimens rendered full barcodes, with four haplotypes showing up to $0.3 \%$ of variation ( $1-2 \mathrm{bp}$ ). Those specimens were compared with one unauthenticated specimen of Pseudapanteles dignus, the only Nearctic species with data available in GenBank. P. gouleti is very distinctive, with more than $18 \%$ of base pairs different from the other species (Fig. 23).

Distribution and biology. All specimens have been collected in an area bounded by the St Lawrence and Ottawa rivers ( $44^{\circ}-46^{\circ} \mathrm{N}$ and $74^{\circ}-75^{\circ} \mathrm{W}$ ) near Canada's capital. This is the northernmost known record of the genus Pseudapanteles. I studied 8 $q$ and 150 captured between mid July to mid September. One specimen was reared from the Maple Leafcutter, Paraclemensia acerifoliella (Fitch, 1856) (Incurvariidae). This is the third record of Braconidae parasitizing an incurvariid Lepidoptera; the other two being another Microgastrinae, Pholetesor ornigis (Weed, 1887), and a Braconinae, Bracon montowesei (Viereck, 1917); in all cases attacking the same incurvariid species (Marsh 1979; Yu et al. 2005; Whitfield 2006).

Etymology. I dedicate this species to Henri Goulet (CNC) in whose backyard (a biodiversity gem in Ottawa, fondly called by CNC researchers as "Goulet National Park") the holotype and several paratypes were collected. Henri wisely encouraged me to study the Microgastrinae and during four years has kindly given me access to his lab, collections and great expertise on many insect topics.

## Venanus heberti Fernández-Triana, sp.n.

urn:lsid:zoobank.org:act:B1DF493F-7D2D-46C4-B7E2-AC26D8EA06FE
Figs 19, 20; Supplementary Appendix 1
Venanus pinicola Mason, 1981: 95 (in part). [Examined].

Type locality. Canada, Prince Edward Island, Blooming Point, $46^{\circ} 24.486^{\prime} \mathrm{N}$, $62^{\circ} 57.062^{\prime} \mathrm{W}$.

Type material. Holotype. Male (CNC), with labels as follows: CANADA: PEI, Blooming Point, $46^{\circ} 24.486^{\prime} \mathrm{N}, 62^{\circ} 57.062^{\prime} \mathrm{W}, 23 . v i i .2008$, fallow field, 6 m , Goulet,

Boudreault \& Badiss, sweeping, \#16. Second label with Specimen ID: MIC 000476. CNC TYPE 23942.

Paratypes (CNC): 1 \& Annapolis Royal, NS, 7.ix.1945, J. McDunnough, ex Microlep. on Gaylussacia; 2 § same data than holotype (Specimen ID: MIC 000474 and MIC 000475); 1 § Bridgetown, NS, 2.ix.12, JES; $1 \delta^{\lambda}$ Sable Island, NS, 11-15. ix.1967, W.R.M. Mason; 1 § Halifax, NS, 15.viii.1954, J. McDunnough, ex Caloptilia asplenifoliella; $1 \circlearrowleft^{\top}$ Knowlton, QC, 19.viii.1929, G. S. Walley, ex larva on Myrica; 1 § Kazabazua, QC, 19.viii.1933, G. S. Walley, ex larva on blueberry.

Diagnosis. $V$. heberti is similar to $V$. pinicola Mason, 1981, and will run to that species in the recent key to the New World species (Whitfield et al., in press). V. pinicola is smaller (females: $1.6-1.9 \mathrm{~mm}$, average $=1.7 \mathrm{~mm}, \mathrm{~N}=8$; males $1.7-2.4 \mathrm{~mm}$, average $=2.0 \mathrm{~mm}, \mathrm{~N}=5$ ) than V . heberti (female: 2.2 mm ; males: $2.0-2.4 \mathrm{~mm}$, average $=2.2, \mathrm{~N}=8$ ). The size (width and height) of the second submarginal cell in the fore wing (compared to the length of vein $r$, the width and the length of stigma) is smaller in $V$. pinicola-usually the values represent $0.6-0.8$ of similar proportions for $V$. heberti. The males of $V$. pinicola have its veins mostly pigmented (as have the females of both species), contrasting with mostly unpigmented veins in males of $V$. heberti. The two species have different geographical distributions: V. pinicola in west Canada/US (AB, BC, YT and ID) and $V$. heberti in Eastern Canada. The known hosts are different: the Gelechids Coleotechnites milleri (Busck, 1914) and C. starki (Freeman, 1957) for V. pinicola; and the Gracillarid Caloptilia asplenifoliella (Darlington, 1949) for V. heberti. The two species also differ in 12 base pairs of the barcode region (more details below under the sections Molecular data, Distribution and biology and Comments).

Description. Male. Antenna length $2.4 \mathrm{~mm}(1.9-2.4 \mathrm{~mm})$, body length 2.4 mm (2.0-2.4 mm), forewing $2.1 \mathrm{~mm}(2.0-2.2 \mathrm{~mm})$. Head with glossa truncate and short. Face smooth, with shallow punctures (separation between punctures larger than punctures diameter) and sparse, uniformly distributed setae. Face width at antennal base/ face width at clypeus edge: $1.1 \times$; intertentorial pit distance/face width at clypeus edge: $0.5 \times$; compound eye height/head height: $0.7 \times$; head height/width: $0.7 \times$; face width at antennal base/head maximum width: $0.6 \times$; malar space/basal width of mandible $1.0 \times$. Clypeus transverse, its width/height: $3.6 \times$. Ocelo-ocular distance/posterior ocelli diameter: $2.0 \times(2.0-2.4 \times)$; distance betwen posterior ocelli/ocelli diameter: $2.0 \times$.

Mesosoma. Pronotum very smooth and polished, laterally with only the ventral groove well defined. Mesoscutum mostly smooth, with shallow but close punctures (distance between punctures $0.5-0.7$ its diameter), punctures a sparser centrally along the posterior margin. Mesoscutum $1.2 \times(1.1-1.2 \times)$ wider than long. Mesoscutum and scutellum covered by sparse, silvered-coloured pilosity (sparser in the scutellum). Scutellum mostly smooth, with a few, shallow, very sparse punctures. Scutellum length/ width at base $1.0 \times$. Scutellar suture width $1 / 7$ scutellum length, with 16 costulae not very well defined. Posterior band of scutellum polished. Scutellar lateral face with the polished area semicircular, $0.3-0.4 \times$ the face height. Mesopleuron smooth and glabrous on most of its surface, with sparse setae and punctures (distance between punctures usually twice or more its diameter) only on the anterior, ventral and posterior
Apanteles fumiferanae (MIC 000265) Paratype
 (MIC 000283) Paratype
Apanteles huberi (MIC 000108) Holotype Apanteles huberi (MIC 000106) Paratype Apanteles huberi (MIC 000107) Paratype Apanteles huberi (MIC 000109) Paratype
21
$22 \longmapsto 0.02$

24

Figures 2I-24. Neighbour-joining trees, K2P distance model. 21 Type material of Apanteles fumiferanae and $A$. huberi $\mathbf{2 2}$ Type material of Apanteles masmithi and authenticated specimens of $A$. cockerelli 23 Type material of Pseudapanteles gouleti and one unauthenticated specimen of P. dignus 24 Type material of Venanus heberti and one authenticated specimen of V. pinicola. Alphanumeric characters between parentheses refer to the specimens Sample ID (see Methods for more details). The number of specimens per species and its Sample IDs are detailed in the Supplementary Appendix 1.
margins. Deep sulcus, with costulae, separating meso and metapleura. Metapleuron setose and punctured along anterior and ventral margins; lower $1 / 4$ of metapleuron rugulose, and with a broad, crenulated sulcus running from lower margin through spiracle. Metapleural carina lamellate and with costulae. Propodeum mostly rugulose, especially on the apical third (which is concave and delimited from the rest of the propodeum
by a vague transverse carina); an obscure longitudinal carinae running centrally from base of propodeum until it reaches the transverse carina; transverse carina intersected posteriorly by several longitudinal, arched ridges radiating from nucha.

Metasoma. Mediotergite 1 widened and rounded apically, with its widest part subapically; basal width/apical width $0.9 \times$; length/apical width 1.5 ; mediotergite 1 rugulose, apical $1 / 4$ with longitudinal striation laterally and two pits at each side of a central, polished area (like a knob) that reaches the posterior margin of tergite. Mediotergite 2 trapezoidal in shape, centrally smooth and polished, laterally rugulose; basal width/ apical width $0.6 \times$; length/apical width $0.6 \times$. Mediotergite 3 twice the length of mediotergite 2 . Mediotergite 3 and following unsculptured, polished and with few, sparse setae mostly along the posterior margin of tergites.

Legs. Metatibial inner spur $1.2 \times$ the length of outer spur, and $0.6 \times$ the length of metatarsomere 1 . Metafemur $2.7 \times$ as long as wide.

Wings. Forewing vein R1a $0.7 \times$ as long as stigma length; length of R1a $2.7 \times$ as long as the distance between its end and the end of 3 RSb. Vein $r 0.6 \times(0.6-0.7 \times)$ the maximum width of stigma. Second submarginal cell height about the same length (or slightly smaller or larger) than vein r length; vein $2 \mathrm{M} 3.0 \times$ as long as vein (RS +M )b and $0.25-0.33 \times$ the stigma length. Edge of vannal lobe of hindwing covex and uniformly setose.

Colour: Mostly black to dark brown; pro- and meso- tibiae and tarsi yellowish brown, as it is apical $0.2 \times$ of metatibia, metatibial spurs, maxillary and labial palps. Wings hyaline, with most of veins transparent or whitish, except for $\mathrm{C}+\mathrm{Sc}+\mathrm{R}, \mathrm{R} 1$, and 2 M can be partially or totally pigmented; stigma brwon.

Female. Similar to male but with antenna ( -1.0 mm ) much shorter than body length $(2.2 \mathrm{~mm})$ and fore wing $(2.0 \mathrm{~mm})$. Antenna with a single row of placodes. Length/width of flagellomeres: 1 st $(1.6 x)$, 2nd ( $1.1 \times$ ), 8th ( $1.1 \times$ ), 14 th ( $1.2 \times$ ), 15 th ( $1.3 \times$ ). Length of flagellomere $2 /$ flagellomere 14: $1.2 \times$. Fore wing with most veins slightly pigmented (light brown in colour), and with larger and taller second submarginall cell (length of vein 2 M half the stigma length, vein 2 M almost twice the length of vein r . Metafemur thicker, $2.1 \times$ as long as wide. Hypopygium not folded nor striate, with slightly pointed tip not protruding beyond apical tergites. Ovipositor sheaths barely exerted from hypopygium, $0.1 \times$ as long as metatibia length; with sparse and minute setae.

Molecular data. Full barcodes of 3 specimens of $V$. heberti and one specimen of the related species V. pinicola were obtained and compared (Fig. 24). The molecular data showed $12(1.86 \%)$ base pairs of difference between the two species.

Distribution and biology. The species is widely distributed in Eastern Canada (QC, NS, PE), where it has been realibly reared from Gracillaria asplenifoliella. In the CNC there is one specimen of $V$. heberti from BC with a label stating it was reared from Caloptilia invariabilis (Braun, 1927). This has to be a labelling mistake because C. invariabilis is only known from Eastern Canada (NS, ON, QC) and US, but has never been recorded from western Nearctic (De Prins and De Prins 2010).

Comments. When Mason (1981) described V. pinicola he mentioned some variations in the specimens from Eastern Canada compared to the West, but considered
that as intraspecific variation. The consistent, though subtle, morphological and molecular differences; different geographical distribution and hosts provide sufficient evidence to consider them as distinct species. Because of the similarities between the two species, four former paratypes of V. pinicola (in the CNC) are here transferred as paratypes of $V$. heberti.

Etymology. I dedicate this species, recognized after DNA barcoding provided a first clue, to Paul Hebert (University of Guelph), as an appreciation for his support; and also for allowing the gathering of thousand of Microgastrinae barcodes -which will hopefully contribute in a significant way to the taxonomy of such a difficult and diverse group.

## Checklist of genera and species of Microgastrinae for Canada and Alaska

## Genus Alphomelon Mason, 1981

This New World endemic genus was recently revised by Deans et al. (2003), but its distribution is mostly tropical and only one species is recorded from Canada. No additional species are expected from the region.

Alphomelon winniewertzae Deans, 2003. ON, QC. Also recorded from ENA and the NEO (Mesoamerica).

## Genus Apanteles Förster, 1862

This is one of the largest genera of Microgastrinae, with 35 species ( 32 of them described) recorded from the region. There are hundreds of unidentified specimens in the CNC and other collections, and the genus will have many more species when further studies can be carried out. Three species are left undescribed here until more studies of the Holarctic species allow establishing their identities with more accuracy. The only comprehensive key to the Nearctic species is in Muesebeck (1922), a relatively useful although outdated work. Mason (1974) and Fernández-Triana and Huber (2010) provided keys to species parasitizing tortricids -but those papers are missing many other species attacking a different spectrum of Lepidoptera. In his review of Apanteles sensu lato Papp (1976) and subsequent papers provided keys to the European species, and Chen and Song (2004) also provided a key to Chinese species. The genus badly needs a comprehensive review and, probably as importantly, a clarification of its current limits, a controversial and unsolved problem (e.g. Mason 1981; Whitfield 1995, 1997; van Achterberg 2002b).

Apanteles aristoteliae Viereck, 1912. NB, ON, QC. Distributed in the NEA. Apanteles baldufi Muesebeck, 1968. ON. Also recorded from MI and MN in US.

Apanteles canarsiae Ashmead, 1898. ON, QC. Distributed in the ENA.
Apanteles carpatus (Say, 1836). BC, NB, ON. A cosmopolitan species.
Apanteles conanchetorum Viereck, 1917. NS, ON. Distributed in the ENA.
Apanteles corvinus Reinhard, 1880. NL. Distributed in the PAL, introduced in Canada (Raske, 1978) to control the birch casebearer moth Coleophora serratella (Coleophoridae).
Apanteles crassicornis (Provancher, 1886). AB, ON, SK, QC. Distributed mostly in the ENA, with some records on CNA and WNA.
Apanteles depressariae Muesebeck, 1931. NS, ON, QC. Distributed in the ENA.
Apanteles edwarsii Riley, 1889. ON, QC. Distributed in the ENA.
Apanteles ensiger (Say, 1836). MB, NS, ON, QC. Distributed in the ENA and CNA.
Apanteles epinotiae Viereck, 1912. ON. Distributed in the ENA and CNA.
Apanteles feltiae Viereck, 1912. SK. Distributed in the NEA.
Apanteles forbesi Viereck, 1910. MB, NS, ON. Distributed in the NEA.
Apanteles fumiferanae Viereck, 1912. AK, BC, MB, NB, NL, NT, ON, QC. Distributed in the NEA, with a record from Europe (Poland). Recent work done on this species has segregated several new species from A. fumiferanae (e.g. Mason 1974; Fernández-Triana and Huber 2010; this study). However, morphology, barcoding, and host data strongly suggest that there are still more species under that name. An integrative approach will be needed to unravel this species-complex. In the meantime, the accuracy of current host records and "species" distribution should be taken with extreme caution. Solving this taxonomic mess will be very important because of the role played in the biological control of economically important pests, especially the tortricid genus Choristoneura.
Apanteles galleriae Wilkinson, 1932. BC. A cosmopolitan species.
Apanteles harti Viereck, 1910. ON. Distributed in the ENA.
Apanteles huberi Fernández-Triana, 2010 [present paper]. BC.
Apanteles jenniferae Fernández-Triana, 2010 [present paper]. NB, ON, QC.
Apanteles laricellae Mason, 1959. NB, ON, QC. Distributed in the ENA.
Apanteles masmithi Fernández-Triana, 2010 [present paper]. ON, NS.
Apanteles milleri Mason, 1974. BC, NB, NT, ON, QC. Distributed in the NEA (across Canada and northern US).
Apanteles morrisi Mason, 1974. BC, MB, NB, ON, QC. Distributed in the HOL (across Canada, northern US and Poland).
Apanteles nephoptericis (Packard, 1864). ON. Distributed in the NEA.
Apanteles petrovae Walley, 1937. AB, BC, NB, NL, ON, QC, SK. Distributed in the HOL. This species has always been considered as belonging to Apanteles by North America authors since its description (e.g. Mason 1974, 1981; Whitfield 1995); however, Papp (1988) transferred it to Dolichogenidea in his treatment of the European species, and that has been accepted by other workers. The generic identity of the species certainly seems controversial from both morphology and molecular data. For example, Nearctic specimens of $A$. petrovae tend to cluster with Dolichogenidea instead of Apanteles (Fernández-Triana, unpublished data).

Even from a detailed morphological redescription of the species (Mason 1974) it could be inferred that the species belongs to Dolichogenidea. However, I have carefully examined the holotype and found that the vannal lobe is medially flattened and with minute, sparse setae; a character that would put the species under the genus Apanteles. As stated before, our present understanding of those genera is far from complete; but pending more studies to clarify or improve the boundaries between them I prefer to keep the traditional treatment of the species as Apanteles.
Apanteles plesius Viereck, 1912. ON. Distributed in the ENA.
Apanteles polychrosidis Viereck, 1912. BC, MB, ON, QC. Distributed in the NEA.
Apanteles roughleyi Fernández-Triana, 2010 [present paper]. BC.
Apanteles samarshalli Fernández-Triana, 2010 [present paper]. ON. Also found in FL. See more comments of its distribution under the species description above.
Apanteles sodalis (Haliday, 1834). BC, NB, NL. Distributed in the HOL, introduced accidentally to Canada (Mason 1978).
Apanteles starki Mason, 1960. AB, BC. Distributed in WNA and China.
Apanteles victoriae Muesebeck, 1921. BC.
Apanteles xanthostigma (Haliday, 1834). NL. Distributed in the PAL and with two references from Uganda (Yu et al. 2009). Introduced in Canada (Williamson 1963), though there is no published data about its establishment.
Apanteles sp. 1 near nephoptericis. ON. Four specimens in CNC. Most likely it is a new species but, pending further study of the Holarctic fauna of Apanteles, it is not described in this paper.
Apanteles sp. 2 near plesius. QC. A recent paper (Fernández-Triana et al. 2009b) recorded three specimens from Frelishburg, QC, as a different but related species.
Apanteles sp. 3 near pseudoglossae. QC. A recent paper (Fernández-Triana et al. 2009b) recorded one specimen from Frelishburg, QC, as A. pseudoglossae Muesebeck, 1921, which would represent a new record of the species for Canada. After checking the specimen and comparing it with other Nearctic material I now consider it a different species. Thus, the known distribution of $A$. pseudoglossae at present does not extend to Canada -as stated by those authors- but it is restricted to IL, MD, MI and MN in the US.

## Genus Choeras Mason, 1981

There are keys to some Palearctic species (e.g. Tobias 1986; van Achterberg 2002a; Chen and Song 2004; Kotenko 2007), although the genus has never been properly revised. Three species are known from the Nearctic region (Whitfield 1995) and all of them occur in Canada. Additionally, in the CNC there are many specimens from western Canada that most likely represent several species; but lacking comprehensive studies of the genus I am taking the conservative approach of keeping them as belonging to one species for now.

Choeras consimilis (Viereck, 1911). MB, NB, ON, QC. Distributed in the HOL. Choeras insignis (Muesebeck, 1938). BC. Also recorded from CA in the US. Choeras tiro (Reinhard, 1880). NL, NS, PE. Distributed in the HOL Choeras sp. AB, BC.

## Genus Clarkinella Mason, 1981

There are only two described species from this genus, one of them from Canada (Mason 1981). I do not expect more species from the region.

Clarkinella canadensis Mason, 1981. ON. Known previously only from holotype, two additional specimens were recently collected in Ottawa.

## Genus Cotesia Cameron, 1891

This is probably the largest genus in the region. It is also one of the most cohesive taxa within Microgastrinae (Mason 1981), although sometimes specimens of Protapanteles (see below on remarks of that genus) could be confused with Cotesia. The keys in Muesebeck (1922) and Papp (1990) will only work partially for identifying specimens, because a plethora of new taxa remain undescribed. Here 55 species are recorded for the region studied ( 51 of them described). At least four undescribed species are also mentioned but lack of a comprehensive study on the Holarctic fauna prevents me to formally describe them here. Additionally, thousands of specimens in collections remain unidentified; some of them likely represent many additional species.

Cotesia acauda (Provancher, 1886). NS, ON, QC. Distributed in the ENA.
Cotesia acronyctae (Riley, 1871). AB, ON, SK. Distributed in the NEA.
Cotesia anisotae (Muesebeck, 1921). NB, ON. Distributed in the NEA.
Cotesia atalantae (Packard, 1881). AB, MB, ON, SK, QC. Distributed in the NEA.
Cotesia autographae (Muesebeck, 1921). NL, MB, QC. Distributed in the NEA.
Cotesia brevicornis (Wesmael, 1837). AB. Distributed in the HOL.
Cotesia carduicola (Packard, 1881). ON. Distributed in the NEA.
Cotesia cerurae (Muesebeck, 1926) ON. QC. Distributed in the ENA.
Cotesia cingiliae (Muesebeck, 1931). AB, BC, NB, NS, ON, QC. Distributed in the ENA.
Cotesia clisiocampae (Ashmead, 1903). ON. Previously known from north-eastern US. First record to Canada.
Cotesia congestiformis (Viereck, 1923). AK.
Cotesia congregata (Say, 1836). MB, NB, ON, PE. Distributed in the NEA and the NEO.
Cotesia crambi (Weed, 1887). QC. Distributed in the ENA.

Cotesia cyaniridis (Riley, 1889). ON, QC. Distributed in the NEA.
Cotesia diacrisiae (Gahan, 1917). ON, QC. Distributed in the NEA.
Cotesia diversa (Muesebeck \& Walkley, 1951). MB. Previously known only from Connecticut, first record to Canada.
Cotesia electrae (Viereck, 1912). BC. Distributed in the NEA and Mexico.
Cotesia enypiae (Mason, 1959). BC.
Cotesia fiskei (Viereck, 1910). AB, BC, MB, NB, NL, NS, ON, SK. Distributed in the US, first record to Canada.
Cotesia flaviconchae (Riley, 1881). ON. Distributed in the US, first record to Canada.
Cotesia flavicornis (Riley, 1889). MB, ON. Distributed in the US, first record to Canada.
Cotesia glomerata (Linnaeus, 1758). BC, NB, ON, QC. A cosmopolitan species.
Cotesia griffini (Viereck, 1911). AB, NB, QC. Distributed in the NEA.
Cotesia halisidotae (Muesebeck, 1931). BC, MB, ON, QC. Distributed in the NEA.
Cotesia hallii (Packard, 1877). NT, NU. Also recorded from Greenland.
Cotesia hemileucae (Riley, 1881). NB. Distributed in the US, first record to Canada.
Cotesia hyphantriae (Riley, 1887). BC, MB, NB, NS, ON, QC. Distributed in the HOL and Mexico.
Cotesia koebelei (Riley, 1889). BC. Distributed in the US, first record to Canada.
Cotesia laeviceps (Ashmead, 1890). AB, BC, MB, NB, ON, QC, SK. Distributed in the NEA.
Cotesia limenitidis (Riley, 1871), NS, ON. Distributed in the NEA.
Cotesia lunata (Packard, 1881). QC. Distributed in the US, first record to Canada.
Cotesia lyciae (Muesebeck, 1938). QC. Previously known only from Maine, first record to Canada.
Cotesia mahoniae (Mason, 1975). BC. Distributed in the WNA.
Cotesia melanoscela (Ratzeburg, 1844). BC, NB, NL, NS, ON, PE, QC. Distributed in the HOL.
Cotesia murtfeldtae (Ashmead, 1898). MB, ON, QC. Distributed in the NEA.
Cotesia nemoriae (Ashmead, 1898). MB, NL, NS, ON, QC, SK. Distributed in the NEA.
Cotesia olenidis (Muesebeck, 1922). BC.
Cotesia parastichtidis (Muesebeck, 1921). BC, NB, NS, ON. Distributed in the NEA.
Cotesia phobetri (Rohwer, 1915). AB, NL, ON. Distributed in the NEA.
Cotesia plathypenae (Muesebeck, 1921). BC, MB. Distributed in the NEA.
Cotesia pyraustae (Viereck, 1912). ON. Distributed in the ENA.
Cotesia pyrophilae (Muesebeck, 1926). ON. Distributed in the ENA.
Cotesia rubecula (Marshall, 1885). BC, ON, QC. A cosmopolitan species.
Cotesia rufocoxalis (Riley, 1881). NS. Distributed in the ENA and CNA.
Cotesia schizurae (Ashmead, 1898). ON. Distributed in the US, first record to Canada.
Cotesia scitula (Riley, 1881). NS, ON. Distributed in the ENA and CNA.
Cotesia smerinthi (Riley, 1881). BC, ON, QC. Distributed in the NEA.
Cotesia teleae (Muesebeck, 1926). AB, BC. Distributed in the US, first record to Canada. The new distribution towards western NEA is significant.


Figure 25. Neighbour-joining tree, K2P distance model, for Cotesia spp. from Canada and Alaska. The tree is cut in two sections to allow its display in a single page. The red square shows the complex of species related to C. xylina and C. yakutatensis (see explanation in the text, Checklist section). The number of specimens per species and its Sample IDs are detailed in the Supplementary Appendix 2.

Cotesia tmetocerae (Muesebeck, 1921). NS.
Cotesia xylina (Say, 1836). AB, MB, NS, ON, QC. Distributed in the NEA. Whether this species is valid or not has been questioned by Muesebeck (1921) and Papp (1986) who considered it a synonym of C. yakutatensis or C. tibialis (Curtis) respectively. Some of the Canadian specimens seem closely related to those of $C$. yakutatensis. However, when barcoded specimens from Canadian C. xylina, C. yakutatensis and related specimens are analyzed, 5 distinct clusters are obtained (Fig. 25; Supplementary Appendix 2). Based on the keys of Muesebeck (1921), Papp (1986, 1987, 1989) and van Achterberg (2006), some of those specimens might be C. halli, C. melanoscela, C. eliniae, C. tetricus (the last two not yet recorded from the Nearctic), or just new species. The only way to solve this species-complex would be a study of the genus at Holarctic level, which is beyond this paper.
Cotesia yakutatensis (Ashmead, 1902). AK, BC, MB, QC. Distributed in the NEA. See comments under C. xylina.
Cotesia sp. 1. MB. This species is treated as Cotesia jft 01 in a paper currently under review (Fernández-Triana et al. unpublished). The only available specimen, a male from Burnt Site, Churchill, MB, runs to C. nemoriae in Muesebeck (1921) and to C. subordinanius in Papp (1986), but it is neither of those species. Its very large metacoxae (half the length of the metasoma) are very distinctive and seem to support its status as a new species.
Cotesia sp. 2. MB, NL, NU, PE, QC, YT. This species is treated as Cotesia jft09 in a paper currently under review (Fernández-Triana et al. unpublished). Additional specimens, mostly from northern localities, have been found later in several Canadian provinces and territories. It is related to Holarctic species with short antennae -e.g. C. arctica (Thompson), C. astrarches (Marshall, 1889), and C. tenebrosa (Wesmael) —but differs from all of the species keyed by Papp (1976). Most likely it is a new species but, pending further study of the Holarctic fauna, it is not described in this paper.
Cotesia sp. 3. AB, MB, ON, SK, YT. The specimens grouped here (in the CNC) comprise those near C. xylina and/or C. yakutatensis that are still unresolved but are clearly different species (Fig. 25; see also comments under C. xylina). I am taking the conservative approach of considering all those specimens as belonging to one species for now -though they most likely represent several.
Cotesia sp 4. ON. Over 30 specimens reared from Plutella xylostella in Ottawa. It is none of the known species of Cotesia parasitizing Plutella, and most likely represents a new species. It is not described here because of the same reason than previous species.

## Genus Deuterixys Mason, 1981

This is a small genus and the Nearctic species were revised by Whitfield (1985). No additional species are expected to be represented in the region.

## Genus Diolcogaster Ashmead, 1900

At least 10 species (7 of them described) are recorded here; however, it is clear that the actual number of species is much higher. For example: based only on the specimens of Diolcogaster with barcode sequences currently available (135 specimens, 122 of them with more than 500 bp ) there are more than 17 clearly delimited species in the region, even if a very conservative approach is taken (Fig. 26; Supplementary Appendix 2). No further efforts are made here to deal with those specimens because there is a pending taxonomic review at Nearctic level (Choi WY and Whitfield JB, unpublished) that should improve our present understanding of the genus.

Diolcogaster auripes (Provancher, 1886) NB, ON, QC. Distributed in the ENA and CNA.
Diolcogaster bakeri (Muesebeck, 1922). ON, QC, SK. Distributed in the NEA and NEO. Recently recorded in Canada (QC) by Fernández-Triana et al. (2009b).
Diolcogaster brevicauda (Provancher, 1886). QC. Distributed in the ENA.
Diolcogaster facetosa (Weed, 1888). AB, BC, ON, QC. Distributed in the NEA and China.
Diolcogaster garmani (Ashmead, 1900). ON. Distributed in the US, first record to Canada.
Diolcogaster schizurae (Muesebeck, 1922). BC, ON. Distributed in the NEA.
Diolcogaster scotica (Marshall, 1885). BC, QC. Distributed in the HOL.
Diolcogaster sp. 1. MB. This species is treated as Diolcogaster jft 01 in a paper currently under review (Fernández-Triana et al. unpublished). It does not key to any described species, and the barcoding data suggests it is one of the most distinctive and unique species within the genus.
Diolcogaster sp 2. AK. This is the first record of the genus for Alaska. The specimen, collected on July, 1959 in Umiat $\left(69^{\circ} 22^{\prime} \mathrm{N}, 152^{\circ} 09^{\prime} \mathrm{W}\right)$ and housed in the CNC is very distinctive and also represents the northernmost known record of the genus.
Diolcogaster sp. 3. NT. One specimen, almost as far north as the previous species, was collected on July, 1971 at Kovaluk River ( $69^{\circ} 11^{\prime} \mathrm{N}, 131^{\circ} 00^{\prime} \mathrm{W}$ ) and housed in the CNC. However, it represents a different species.

## Genus Distatrix Mason, 1981

This is a predominantly tropical genus, and a revision of the New World species was published recently (Grinter et al. 2009). I have found a new species reaching as north as QC, Canada, and representing the northernmost known record.

Distatrix carolinae Fernández-Triana, 2010 [present paper]. QC.


Figure 26. Neighbour-joining tree, K2P distance model, for Diolcogaster spp. from Canada and Alaska. The species are not named pending an upcoming review of the genus (Choi WY and Whitfield JB, unpublished). The number of specimens per species and its Sample IDs is detailed in the Supplementary Appendix 2.

Genus Dolichogenidea Viereck, 1911

The keys dealing with Apanteles (mentioned above in the treatment of that genus) also cover the species of Dolichogenidea. Both genera are easily confused (Mason 1981; Whitfield et al. 2009), and the correct generic assignment of some of the species is often limited by subtle and subjective characters. A comprehensive study of those genera (plus a few others, see for example, van Achterberg 2002b) is badly needed to redefine
its limits with accuracy. In the meantime, 19 species of Dolichogenidea (17 of them described) are recorded here for the region studied.

Dolichogenidea absona Muesebeck, 1965. AB, BC, NB, NL, NS, MB, ON, PE, QC. Distributed in the NEA.
Dolichogenidea breviventris (Ratzeburg, 1848). Previously recorded as D. mesoxantha (Ruschka, 1971) by Whitfield (1995) in his list of Nearctic species. However, D. mesoxantha was synomized under D. breviventris by Papp (1978). NL. Distributed in the HOL.
Dolichogenidea cacoeciae (Riley, 1881). ON, QC. Distributed in the NEA.
Dolichogenidea californica (Muesebeck, 1921). AB, BC, ON, QC. Distributed in the WNA, here recorded for the first time from ENA.
Dolichogenidea clavata (Provancher, 1881). ON, QC. Distributed in the NEA.
Dolichogenidea coleophorae (Wilkinson, 1938). NL. Distributed in the PAL, introduced in Canada. In the CNC there are specimens reared in NL from the birch casebearer moth Coleophora serratella (Coleophoridae). This species was transferred to Apanteles by van Achterberg (2002b) but I am keeping it as Dolichogenidea based on its vannal lobe medially convex and uniformly covered by setae of the same length.
Dolichogenidea homoeosomae (Muesebeck, 1933). SK. Distributed in the NEA and Cuba.
Dolichogenidea lacteicolor (Viereck, 1911). NB, NS, QC. Distributed in the HOL and also some records in the Oriental region. This species was transferred to Apanteles by van Achterberg (2002b) but I am keeping it as Dolichogenidea based on its vannal lobe medially convex and uniformly covered by setae of the same length.
Dolichogenidea laspeyresiae (Viereck, 1913). BC. Distributed in the WNA.
Dolichogenidea longicauda Wesmael (1837). BC. Distributed in the HOL. Recently Fernández-Triana and Huber (2010) commented on the changing generic status of this species within the last years, and considered it as belonging to Dolichogenidea, a decision that is followed here.
Dolichogenidea melanopa (Viereck, 1917). BC, PE. Previously known from Connecticut. First record to Canada.
Dolichogenidea paralechiae (Muesebeck, 1932). NB, ON, QC. Distributed in the NEA.
Dolichogenidea phthorimaeae (Muesebeck, 1921). ON. Distributed in the NEA and Honduras.
Dolichogenidea renaulti Mason, 1974. NB, NS, ON, QC. Distributed in the ENA.
Dolichogenidea solenobiae (Walley, 1935). ON, QC. Distributed in the ENA.
Dolichogenidea thujae (Muesebeck, 1935). ON, QC. Distributed in the ENA.
Dolichogenidea tischeriae (Viereck, 1912). QC. Distributed in the NEA. A recent paper (Fernández-Triana et al. 2009b) recorded the species for the first time in Canada, but erroneously mentioned it as Apanteles tischeriae. The species was transferred to Dolichogenidea by Mason (1981).
Dolichogenidea sp. 1 near cacoeciae. BC. Twelve specimens in the CNC were considered by Mason as a different species. Pending further study of the Holarctic fauna of Dolichogenidea, it is not described in this paper.

Dolichogenidea sp. 2. ON. Considered by Mason as a new species belonging to the Dolichogenidea laevigata species-group. The CNC has 14 specimens that were reared from two Tortricidae hosts: Proteotera aesculana (4 specimens) and Argyroploce albiciliana (10 specimens). Pending further study of the Holarctic fauna of Dolichogenidea, it is not described in this paper.

## Genus Exix Mason, 1981

This genus has one Nearctic species (Mason 1981), known from only one specimen in Canada.

Exix columbica Mason, 1981. BC.

## Genus Exoryza Mason, 1981

Like the previous genus, only one species is known from the Nearctic (Mason 1981), with no more species seen in collections (Whitfield 1995).

Exoryza minnesota Mason, 1981. ON. Distributed in the ENA.

## Genus Glyptapanteles Ashmead, 1904

This genus is considered one of the most diverse and dominant genera in tropical regions (e.g. Whitfield 1995; Whitfield et al. 2009), but is still very commonly seen and specious in Alaska/Canada, reaching even to the tip of Ellesmere Island $\left(+82^{\circ} \mathrm{N}\right)$. Papers covering Apanteles (mentioned above under that genus) will deal with some species, but the limits of the genus are controversial (e.g. van Achterberg 2002b; and discussion under Protapanteles below) and there are no updated keys to the species. Many unidentified specimens remain in collections and the recorded species here (10, nine of them described) are just a fraction of the actual number.

Glyptapanteles alticola (Ashmead, 1902). AK, BC, NB. Distributed in the NEA. From the material housed in the CNC, Papp's (1983) statement that G. alticola is not different from G. fulvipes (Haliday) seems valid. However, both species are kept here as valid until the type material can be studied.
Glyptapanteles compressiventris (Muesebeck, 1921). MB, NT, NU, QC. Distributed in the HOL.
Glyptapanteles flavovariatus (Muesebeck, 1921). BC, ON. Distributed in the NEA. First record to Canada.

Glyptapanteles fulvipes (Haliday, 1834). AB, NT, NU, QC. Distributed in the HOL. First record to Canada.
Glyptapanteles militaris (Walsh, 1861). MB, NB, ON, QC. A cosmopolitan species.
Glyptapanteles pallipes (Reinhard, 1880). AK, BC, NB, ON, QC. A cosmopolitan species. I am including under this species also G. longicornis (Provancher, 1886), a name mentioned as a valid species by Whitfield (1995) in his list of Nearctic species. However, G. longicornis was synonymized under G. pallipes by Papp (1988), an arrangement that has been accepted by subsequent authors (e.g. Yu et al. 2005; Kotenko 2007).
Glyptapanteles sarrothripae (Weed, 1887). BC, NS, ON. Distributed in the ENA, here recorded for the first time for WNA.
Glyptapanteles websteri (Muesebeck, 1921). AB, NB, QC. Distributed in the ENA.
Glyptapanteles sp. 1 near alticola. MB. Specimens from Manitoba form around half a dozen of distinct clusters based in barcoding data that might well represent different species related to G. alticola (Fernández-Triana et al. unpublished data). The barcoding differences are also supported by slight morphological differences (e.g. antennae colour, relative length of the last flagellomeres, puncture density of head, seta density and length on the mesoscutum, scutellum punctures, wing base colour, propodeal carination, hind leg colour -especially tibia and tarsi- sculpture of mediotergites 1 and 2). However, without having molecular data from the type material and/or a comprehensive taxonomical review of the genus within the Holarctic, an unequivocal assignment of specimens is not possible at present. I am taking the conservative approach of considering all specimens as one species for now -though they probably represent many species.

## Genus Hygroplitis Thomson, 1895

No more species are expected to be found within the Nearctic region (Whitfield 1995).
Hygroplitis melligaster (Provancher, 1886). MB, NB, NS, ON, QC. Distributed in the ENA, here recorded for the first time from CNA.

## Genus Hypomicrogaster Ashmead, 1898

Some specimens in the CNC seem to be different species than the two described species here recorded for the region. There is currently a review of the genus underway for the New World fauna (Valerio A, pers. com.) and thus no further attempt is made here to deal with those unidentified specimens.

Hypomicrogaster ecdytolophae (Muesebeck, 1922). NS, ON, QC. Distributed in the NEA and the NEO.

Hypomicrogaster zonaria (Say, 1836). NB, NS, ON, QC. Distributed in the NEA Hypomicrogaster sp. ON. This is a new species that will be described elsewhere (Valerio A, pers. com.).

## Genus Iconella Mason, 1981

This genus has never been revised, though key to some Palearctic species can be found in Chen and Song (2004) and Kotenko (2007). There is only one described species within the Nearctic (from US and the Neotropics) but none was previously recorded from Canada. I have found at least two species in Canada but, pending a study of the Holarctic fauna, the species are not described here.

Iconella sp. 1. NB. In the CNC.
Iconella sp. 2. ON, BC. In the CNC.

## Genus Illidops Mason, 1981

This genus has never been revised, though Kotenko (2007) provided a key to the Russian Far East. There is only one described species within the Nearctic (from southern US) and a few undescribed have been mentioned from Arctic Canada and the Rocky Mountains (Mason 1981). Some of the Canadian species lack the posterior medioapically desclerotized tergites and/or the convergent eyes that characterize the genus. The majority of the specimens available were collected more than 30 years ago, and only one recent specimen rendered a full barcode, but for 18 older specimen partial barcodes (120-292 bp) were obtained. Both morphology studies and barcoding indicate that, even under the most conservative approach, there are at least four species in the studied region. Pending a larger study of the Holarctic fauna, the species are not described here.

Illidops sp. 1. MB. This species is treated as Illidops jft 01 in a paper currently under review (Fernández-Triana et al. unpublished).
Illidops sp. 2. MB. This species is treated as Illidops jft 02 in a paper currently under review (Fernández-Triana et al. unpublished).
Illidops sp. 3. MB. This species is treated as Illidops jft 03 in a paper currently under review (Fernández-Triana et al. unpublished).
Illidops sp. 4. AB, MB, NS, NT, ON, QC. Additional material from the provinces mentioned here is housed in the CNC. They are different from the previous three species, and probably represent more than one species, but for now are kept provisionally as one species.

## Genus Lathrapanteles Williams, 1985

This genus was described and its species revised by Williams (1985) and no new additions are expected. The validity and relationships of this genus to other Microgastrinae might be questioned when future studies are made.

Lathrapanteles fuscus Williams, 1985. BC, MB, NS, NT, QC. Distributed in the NEA. Lathrapanteles heleios Williams, 1985. ON.
Lathrapanteles papaipemae (Muesebeck, 1921). NL, ON, QC. Distributed in the NEA.

## Genus Microgaster Latreille, 1804

Muesebeck (1922), Nixon (1968) and Papp (1984) provided keys covering all known species of the region, and Whitfield (1995) estimated that only a handful of species were likely to be added to the Nearctic though he also remarked the need for a full appraisal of the North American fauna. Here I consider 13 species for Canada/Alaska, two of them needing further study to clarify their specific status.

Microgaster brittoni Viereck, 1917. ON. Distributed in the ENA.
Microgaster canadensis Muesebeck, 1922. AB, BC, MB, NB, NS, ON, PE, QC, SK. Distributed in the NEA.
Microgaster congregatiformis Viereck, 1917. AB, MB, ON. Distributed in the NEA. Microgaster deductor Nixon, 1968. MB. Distributed in the PAL, recorded from Canada in a paper currently under review (Fernández-Triana et al. unpublished).
Microgaster epagoges Gahan, 1917. BC, ON, QC. Distributed in the NEA.
Microgaster gelechiae Riley, 1869. ON, QC. Distributed in the NEA.
Microgaster hospes Marshall, 1885. ON, QC. Distributed in the HOL.
Microgaster leechi Walley, 1935. BC, MB, ON, QC. Distributed in the NEA.
Microgaster pantographae Muesebeck, 1922. ON. Distributed in the HOL.
Microgaster peroneae Walley, 1935. AK, BC, NB, NL, NS, ON, QC. Distributed in the NEA.
Microgaster messoria Haliday, 1834. ON, QC. Distributed in the HOL, was introduced in the NEA at the beginning of the XX century.
Microgaster sp. 1. MB. This species is treated as Microgaster jft 01 in a paper currently under review (Fernández-Triana et al. unpublished). The only specimen available, a male, appears related to M. sticticus Ruthe, 1858 (from the Palearctic region) but more material is needed before its status can be clearly defined.
Microgaster sp. 2. MB. This species is treated as Microgaster jft 02 in a paper currently under review (Fernández-Triana et al. unpublished). The small size (about 2.5 mm ), eyes subparallel, mesoscutum rugulose and small length of ovipositor make this species related to the European $M$. fischeri Papp, 1960, but it is most likely a new species.

## Genus Microplitis Förster, 1862

This is a diverse genus in the Holartic, and there are no satisfactory keys to species available. Whitfield (1995) estimated that more than half of the Nearctic species were undescribed. Indeed, there are hundreds of specimens in collections that likely represent many new species. Here I report 21 species ( 19 of them described), but this is just a fraction of the actual number. Barcoding data available for 681 specimens with more than 500 bp (Supplementary Appendix 3) reveals almost 60 species, even under the most conservative approaches.

Microplitis alaskensis Ashmead, 1902. AK, AB, BC, MB, NS, ON, QC. Distributed in the NEA.
Microplitis autographae Muesebeck, 1922. AB, ON. Distributed in the CNA. Microplitis bradleyi Muesebeck, 1922. AB, BC. Distributed in the WNA.
Microplitis carteri Walley, 1932. AB.
Microplitis ceratomiae Riley, 1881. NB, NS, ON, QC, SK. Distributed in the NEA.
Microplitis confusus Muesebeck, 1922. NB, ON. Distributed in the NEA.
Microplitis crenulatus (Provancher, 1888). QC. Distributed in the ENA.
Microplitis gortynae Riley, 1881. ON. Distributed in the NEA.
Microplitis hyphantriae Ashmead, 1898. AB, ON, QC. Distributed in the NEA.
Microplitis impressus (Wesmael, 1837). MB, ON, QC. Distributed in the HOL.
Microplitis kewleyi Muesebeck, 1922. AB, MB, NB, ON, QC. Distributed in the NEA.
Microplitis laticinctus Muesebeck, 1922. QC. Distributed in the ENA.
Microplitis mamestrae Weed, 1887. BC. Distributed in the NEA.
Microplitis maturus Weed, 1888. BC, ON, QC. Distributed in the ENA and CNA.
Microplitis melianae Viereck, 1911. AB, ON. Distributed in the NEA.
Microplitis plutellae Muesebeck, 1922. ON, QC, SK. Distributed in the HOL.
Microplitis quadridentatus (Provancher, 1886). ON. Distributed in the ENA.
Microplitis scutellatus Muesebeck, 1922. AB. Distributed in the NEA.
Microplitis varicolor Viereck, 1917. MB, NB, ON, QC. Distributed in the NEA.
Microplitis sp. 1. MB. This species is treated as Microplitis jft01 in a paper currently under review (Fernández-Triana et al. unpublished). Without study of authenticated material from Europe is difficult to conclude, but according to the descriptions provided by Papp (1984) and van Achterberg (2006) this species is closely related to M. coactus (Lundbeck, 1896), which was previously known just from Greenland and Iceland. The specimens from Churchill may represent a different and new species, with larger metafemur.
Microplitis sp. 2 near varicolor. MB. There are numerous specimens in the CNC that are related to $M$. varicolor but seem different species -based on both barcoding and morphological differences. A comprehensive study of Microplitis at least at Nearctic level will be needed before those specimens can be assigned to species.

## Genus Paroplitis Mason, 1981

There is only one known Nearctic species and no more are expected (Mason 1981; Whitfield 1995).

Paroplitis beringianus Mason, 1981. AK, BC.

## Genus Pholetesor Mason, 1981

The Nearctic species were revised by Whitfield (2006) and the genus is reasonably covered. However, Palearctic species need to be dealt with altogether with the Nearctic ones to avoid duplication of descriptions. For that reason, I am treating two of the 20 species recorded here as undescribed for now.

Pholetesor bedelliae (Viereck, 1911). BC, NS, ON, QC. A cosmopolitan species.
Pholetesor caloptiliae Whitfield, 2006. ON. Distributed in the ENA.
Pholetesor circumpscriptus (Nees, 1834). AK. A cosmopolitan species.
Pholetesor glacialis (Ashmead, 1902). AK, BC.
Pholetesor longicoxis Whitfield, 2006. QC. Distributed in the ENA.
Pholetesor masneri Mason, 1981. ON. Distributed in the ENA.
Pholetesor masoni Whitfield, 2006. AB, BC, NS, ON, QC. Distributed in the NEA and Mexico.
Pholetesor ornigis (Weed, 1887). MB, NB, NS, ON. QC. Distributed in the NEA.
Pholetesor pedias (Nixon, 1973). ON. Van Achterberg (1997) synonymised this species under P. exiguus (Haliday, 1837) but a latter comprehensive review of Nearctic Pholetesor (Whitfield 2006) kept the P. pedias name. Distributed in the HOL.
Pholetesor pinifoliellae Whitfield, 2006. ON, QC. Distributed in the NEA.
Pholetesor rhygoplitoides Whitfield, 2006. ON, QC. Distributed in the NEA.
Pholetesor rohweri (Muesebeck, 1921). NB, ON. Distributed in the ENA.
Pholetesor salalicus (Mason, 1959). BC. Distributed in the HOL.
Pholetesor salicifoliellae (Mason, 1959). BC, MB, NB, NS, ON, QC. Distributed in the NEA.
Pholetesor thuiellae Whitfield, 2006. NB, ON, QC. Distributed in the ENA.
Pholetesor variabilis Whitfield, 2006. AB, BC, ON, SK. Distributed in the NEA.
Pholetesor viminetorum (Wesmael, 1837). AB, AK, BC, MB, NS, YT. Distributed in the HOL.
Pholetesor zelleriae Whitfield, 2006. MB, ON, QC. Distributed in the NEA.
Pholetesor sp. 1. MB. This species is treated as Pholetesor jft01 in a paper currently under review (Fernández-Triana et al. unpublished). This is likely a new species related to $P$. powelli, P. bedelliae and P. thuiellae but clearly different from them. A study within the context of Holarctic species is badly needed.

Pholetesor sp. 2. MB. This species is treated as Pholetesor jft02 in a paper currently under review (Fernández-Triana et al. unpublished). Two male specimens (Sample ID: 07PROBE-22417, 07PROBE-23399) differ slightly from P. viminetorum regarding veins $r$ and $2 R S$, length of metatibial spurs and shape of tergite 1 and 2. The barcode variation between these two species was $1.94 \%$, and there are also two character states differences within the D2 region of the nuclear gene 28S. The combination of these three lines of evidence suggests that those males are a separate species from P. viminetorum. However, pending a study of the Holarctic fauna, the species is not described here.

## Genus Protapanteles Ashmead, 1898

Altogether with Apanteles, the limits of this genus are one of the most controversial (e.g. Mason 1981; Whitfield 1995, 1997; van Achterberg 2002b; Yu et al. 2005). Mason (1981) provided some characters that supposedly defined the genera, but even within a geographical restricted area such as Canada, there are considerable variation (e.g. specimens with propodeum sculptured like a typical Cotesia, instead of smooth; mediotergite 1 strongly narrowing toward apex like typical Glyptapanteles; specimens looking like Sathon; etc). The North American workers have usually considered it to be a rather small genus, and have kept the other genera separated, but I am not sure if that is the best arrangement, or at least Glyptapanteles and Sathon should be part of an expanded Protapanteles genus -similar to the proposal of van Achterberg (2002b). Solving those problems is beyond the scope of this paper and for now I am following Whitfield's (1995) arrangement of the Nearctic species.

Protapanteles alaskensis (Ashmead, 1902). AK, BC, MB, NL. Distributed in the NEA. Protapanteles paleacritae (Riley, 1881). BC, MB, NL, NS, ON. Distributed in the NEA.
Protapanteles phigaliae (Muesebeck, 1919). NB, ON. Distributed in the NEA.
Protapanteles phlyctaeniae (Muesebeck, 1929). ON. Distributed in the ENA and CNA. Protapanteles sp. 1. AB, BC, SK, MB. A significant number of specimens from western Canada is included here, most of them from reared material housed in the CNC and the Northern Forestry Centre, Edmonton. I am taking the conservative approach of considering all specimens as one species for now -though they likely represent several species

## Genus Protomicroplitis Ashmead, 1898

This small genus had been reported within the Nearctic from central and eastern US, as north as NY (Yu et al. 2005). In the CNC there are several specimens of P. calliptera captured near Ottawa (Metcalfe and Stittsville) which represent the first record of the
genus for Canada and the northernmost distribution in North America. No more species are expected to be found in the region.

Protomicroplitis calliptera (Say, 1836). ON. Distributed in the NEA.

## Genus Pseudapanteles Ashmead, 1898

This New World genus is mostly found in the tropics, with a few species reaching to the US. Here I record two species (one of them new) for Canada, expanding further north the known distribution of the genus.

Pseudapanteles gouleti Fernández-Triana, 2010 [present paper]. ON, QC.
Pseudapanteles sesiae (Viereck, 1912). ON. Two specimens from Niagara Falls represent the northernmost record of the species. Distributed in the NEA.

## Genus Rasivalva Mason, 1981

All the Nearctic species of this genus are dealt with in Muesebeck (1922), and Whitfield (1995) stated that no clearly undescribed species had been seen in collections. I report here an additional undescribed Canadian species that does not fit within the described ones.

Rasivalva perplexa (Muesebeck, 1922). BC, NB, ON. Distributed in the NEA.
Rasivalva rugosa (Muesebeck, 1922). ON, QC. Distributed in the NEA. New record to Canada.
Rasivalva stigmatica (Muesebeck, 1922). AB, BC, QC. Distributed in the NEA. New record to Canada.
Rasivalva sp. ON, NB. Two female specimens in the CNC that are different to the previous species but that are not dealt with further until a study of the Holarctic fauna is done.

## Genus Sathon Mason, 1981

The limits of this genus are controversial (see above comments under Protapanteles and also Whitfield et al. 2002, 2009). Williams (1985) provided a key to species.

Sathon cinctiformis (Viereck, 1911). ON, QC. Distributed in the ENA.
Sathon masoni (Williams, 1988). AK, NU, NT. Distributed in the NEA.
Sathon neomexicanus (Muesebeck, 1921). AB, AK, BC, MB, NL, NT, ON, PE. Distributed in the NEA.
Sathon papilionae (Williams, 1988). AK, BC.

## Genus Venanides Mason, 1981

A small genus with four described species, one of them from the Nearctic (Mason 1981); with an additional couple of undescribed ones in southern US (Whitfield 1995). It is not likely that more species will be found in Canada/Alaska.

Venanides xeste (Mason, 1981). MB, ON. Distributed in the NEA and Brazil.

## Genus Venanus Mason, 1981

The genus was recently revised by Whitfield et al. (in press), but from the seven recognized species within the New World, only one was recorded from the Nearctic. The barcoding data revealed a new species that had been overlooked by Mason (1981); it is clear now that the specimens from eastern and western Canada are different (see more comments on the two species in the section describing the new species).

Venanus pinicola (Mason, 1981). AB, BC, YT. Distributed in the WNA. Venanus heberti Fernández-Triana, 2010 [present paper]. NS, QC, PE.

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## References

Achterberg C van (2002a) Apanteles (Choeras) gielisi spec. nov. (Hymenoptera: Braconidae: Microgastrinae) from The Netherlands and the first report of Trichoptera as host of Braconidae. Zoologische Mededelingen Leiden 76: 1-16.
Achterberg C van (2002b) Western Palaearctic genera of the subfamily Microgastrinae: a reappraisal of the generic and tribal division (Hymenoptera: Braconidae). In: Melika G, Thuróczy G (Eds) Parasitic wasps: evolution, systematics, biodiversity and biological control. Agroinform, Budapest, Hungary, 19-35.
Achterberg C van (2004) Fauna Europaea: Microgastrinae. Fauna Europaea version 1.1, http:// www.faunaeur.org [accessed 1.VIII.2010]
Achterberg C van (2006) The Braconidae (Hymenoptera) of Greenland. Zoologische Mededelingen Leiden 80-1 (2): 13-62.
Biological Survey of Canada (2010) Briefs. Insects of Canada. A synopsis prepared for delegates to the XVIIIth International Congress of Entomology (Vancouver, 1988). http://www. biology.ualberta.ca/bsc/briefs/brinsectsofcane.htm [accessed 1.VIII.2010]
Broad GR, Shaw MR, Godfray HCJ (2009) Checklist of British and Irish Braconidae (Hymenoptera). http://www.nhm.ac.uk/resources-rx/files/braconidae-checklist-final-34139.pdf [accessed 1.VIII.2010]
Chen J, Song D (2004) Systematic studies on Microgastrinae of China (Hymenoptera: Braconidae). Fujian Scientific Publisher, Fuchow, China, 354 pp.
Danks HV (1981) Artic Arthropods: A review of systematics and ecology with particular reference to the North American fauna. Entomological Society of Canada, Ottawa, Canada, 608 pp.
Deans AR, Whitfield JB, Janzen DH (2003) Taxonomy and natural history of the microgastrine genus Alphomelon Mason (Hymenoptera: Braconidae). Journal of Hymenoptera Research 12: 1-41.
De Prins J, De Prins W (2010) Global Taxonomic Database of Gracillariidae (Lepidoptera). http://gc.bebif.be [accessed 1.VIII.2010]
Dolphin K, Quicke DLJ (2001) Estimating the global species richness of an incompletely described taxon: an example using parasitoid wasps (Hymenoptera: Braconidae). Biological Journal of the Linnean Society 73: 279-286.
Fernández J (2007) An overview and update of the Microgastrinae (Hymenoptera: Braconidae) holdings in the Canadian National Collection, Ottawa. Newsletter of the Biological Survey of Canada (Terrestrial Arthropods) 26(2): 51-54.
Fernández-Triana J, Boudreault C, Goulet H (2009a) Revisiting the Northern Insect Survey: Preliminary Results for Microgastrinae Wasps (Hymenoptera: Braconidae). Newsletter of the Biological Survey of Canada (Terrestrial Arthropods) 28(1): 21-25.
Fernández-Triana J, Goulet H, Bostanian N, Boudreault C (2009b) Diversity of Microgastrinae (Hymenoptera: Braconidae) in apple orchards of southern Quebec, Canada. Biocontrol Science and Technology 19(3): 237-248.
Fernández-Triana J, Huber JT (2010) Braconid parasitoids (Hymenoptera: Braconidae) of Nearctic Choristoneura species (Lepidoptera: Tortricidae), with a summary of other parasitoid families attacking Choristoneura. The Canadian Entomologist 142: 295-343.

Freeman TN (1967) On coniferophagous species of Choristoneura (Lepidoptera: Tortricidae) in North America. I. Some new forms of Choristoneura allied to C. fumiferana. The Canadian Entomologist 99: 449-455. doi: 10.4039/Ent99449-5.
Grinter C, Whitfield JB, Connahs H, Dyer LA, Hallwachs W, Janzen DH (2009) A key to Neotropical Distatrix Mason (Hymenoptera: Braconidae), with descriptions of six new reared species. Journal of Insect Science 9 (25): 1-17.
Huber JT, Sharkey MJ (1993) Structure. In Goulet H, Huber JT (Eds) Hymenoptera of the world: an identification guide to families. Agriculture Canada Research Branch, Monograph No. 1894E, Ottawa, Canada, 13-59.
Ivanova NV, Dewaard JR, Hebert PDN (2006) An inexpensive, automation-friendly protocol for recovering high-quality DNA. Molecular Ecology Notes 6(4): 998-1002.
Janzen DH, Hallwachs W, Blandin P, Burns JM, Cadiou J-M, Chacon I, Dapkey T, Deans AR, Epstein ME, Espinoza B, Franclemont JG, Haber WA, Hajibabaei M, Hall JPW, Hebert PDN, Gauld ID, Harvey DJ, Hausmann A, Kitching IJ, LaFontaine D, Landry J-F, Lemaire C, Miller JY, Miller JS, Miller L, Miller SE, Montero J, Munroe E, Green SR, Ratnasingham S, Rawlins JE, Robbins RK, Rodriguez JJ, Rougerie R, Sharkey MJ, Smith MA, Solis MA, Sullivan JB, Thiaucourt P, Wahl DB, Weller SJ, Whitfield JB, Willmott KR, Wood DM, Woodley NE, Wilson JJ (2009) Integration of DNA barcoding into an ongoing inventory of tropical complex biodiversity. Molecular Ecology Resources 9 (supplement 1): 1-26.
Jones OR, Purvis A, Baumgart E, Quicke DLJ (2009) Using taxonomic revision data to estimate the geographic and taxonomic distribution of undescribed species richness in the Braconidae (Hymenoptera: Ichneumonoidea). Insect Conservation and Diversity 2: 204-212.
Kimura M (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. Journal of Molecular Evolution 16(2): 111-20.
Kotenko AG (2007) Microgastrinae. In: Lelej AS (Ed) Key to the insects of Russia Far East. Vol.IV. Neuropteroidea, Mecoptera, Hymenoptera. Pt 5. Dalnauka, Vladivostok, Russia, 134-192.
Lafontaine JD (1997) Butterflies and Moths (Lepidoptera). In: Smith IM (Ed) Assessment of Species Diversity in the Mixedwood Plains Ecozone. Ecological Monitoring and Assessment Network. http://www.naturewatch.ca/mixedwood/lep/intro.htm\#toc [accessed 1.VIII.2010]

Lafontaine JD, Wood DM (1997) Butterflies and Moths (Lepidoptera) of the Yukon. In Danks HV, Downes JA (Eds) Insects of the Yukon. Biological Survey of Canada (Terrestrial Arthropods), Ottawa, Canada, 723-785.
Marsh PM (1979) Braconidae. Aphidiidae. Hybrizontidae. In: Krombein KV, Hurd Jr. PD, Smith DR, Burks BD (Eds) Catalog of Hymenoptera in America north of Mexico. Smithsonian Institution Press, Washington, US, 144-313.
Mason WRM (1974) The Apanteles species (Hymenoptera: Braconidae attacking Lepidoptera in the micro-habitat of the spruce budworm (Lepidoptera: Tortricidae). Canadian Entomologist 106: 1087-1102.
Mason WRM (1978) Ichneumonoid parasites (Hymenoptera) accidentally introduced into Canada. Canadian Entomologist 110: 603-608.

Mason WRM (1981) The polyphyletic nature of Apanteles Foerster (Hymenoptera: Braconidae): A phylogeny and reclassification of Microgastrinae. Memoirs of the Entomological Society of Canada 115: 1-147.
Muesebeck CFW (1921) A revision of the North American species of ichneumon-flies belonging to the genus Apanteles. Proceedings of the United States National Museum 58: 483-576
Muesebeck CFW (1922) A revision of the North American ichneumon-flies, belonging to the subfamilies Neoneurinae and Microgasterinae. Proceedings of the United States National Museum 61(2436): 1-76.
Nixon GEJ (1968) A revision of the genus Microgaster Latreille (Hymenoptera: Braconidae). Bulletin of the British Museum (Natural History), Entomology series 22: 33-72.
Papp J (1978) A survey of the European species of Apanteles Först. (Hymenoptera, Braconidae: Microgasterinae), II. The laevigatus-group, 1. Annales Historico-Naturales Musei Nationalis Hungarici 70: 265-301.
Papp J (1983) A survey of the European species of Apanteles Först. (Hymenoptera, Braconidae: Microgastrinae), VII. The carbonarius-, circumscriptus-, fraternus-, pallipes-, parasitellae-, vitripennis-, liparidis-, octonarius- and thompsoni- group. Annales Historico-Naturales Musei Nationalis Hungarici 75: 247-283.
Papp J (1984) Palaearctic species of Microgaster Latreille (= Microplitis Förster) with description of seven new species (Hymenoptera, Braconidae, Microgastrinae). Entomologische Abhandlungen 47: 95-140.
Papp J (1986) A survey of the European species of Apanteles Först. (Hymenoptera, Braconidae: Microgastrinae). IX. The glomeratus-group, 1. Annales Historico-Naturales Musei Nationalis Hungarici 78: 225-247.
Papp J (1987) A survey of the European species of Apanteles Förster (Hymenoptera, Braconidae: Microgastrinae), X. The glomeratus-group 2 and the cultellatus-group. Annales HistoricoNaturales Musei Nationalis Hungarici 79: 207-258.
Papp J (1988) A survey of the European species of Apanteles Först. (Hymenoptera, Braconidae: Microgastrinae). 11. "Homologization" of the species-groups of Apanteles s.l. with Mason's generic taxa. Checklist of genera. Parasitoid/host list 1. Annales Historico-Naturales Musei Nationalis Hungarici 80: 145-175.
Papp J (1989) Contribution to the Braconid wasp of Greenland, Denmark (Hymenoptera: Braconidae). Folia Entomologica Hungarica 100: 95-104.
Papp J (1990) A survey of the European species of Apanteles Först. (Hymenoptera, Braconidae: Microgastrinae) XII. Supplement to the key of the glomeratus-group. Parasitoid/host list 2. Annales Historico-Naturales Musei Nationalis Hungarici 81: 159-203.
Sharkey MJ, Wharton RA (1997) Morphology and terminology. In Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication No. 1, International Society of Hymenopterists, Washington, D.C., 19-63.

Smith MA, Rodriguez JJ, Whitfield JB, Deans AR, Janzen DH, Hallwachs W, Hebert PDN (2008) Extreme diversity of tropical parasitoid wasps exposed by iterative integration of natural history, DNA barcoding, morphology, and collections. Proceedings National Academy of Sciences 105 (34): 12359-12364.

Tamura K, Dudley J, Nei M, Kumar S (2007) MEGA4: Molecular Evolutionary Genetics Analysis (MEGA) software version 4.0. Molecular Biology and Evolution 24: 1596-1599.
Tobias VI (1986) Acaeliinae, Cardiochilinae, Microgastrinae, Miracinae. Supplement. In: Medvedev GS (Ed) Keys to the insects of the European part of USSR (Hymenoptera). 336-501.
Valerio AA, Whitfield JB, Janzen DH (2009) Review of world Parapanteles Ashmead (Hymenoptera: Braconidae: Microgastrinae), with description of fourteen new Neotropical species and the first description of the final instar larvae. Zootaxa 2084: 1-49.
Whitfield JB (1985) The nearctic species of Deuterixys Mason (Hymenoptera: Braconidae). Pan-Pacific Entomologist 61: 60-67.
Whitfield JB (1995) Checklist of the Microgastrinae (Hymenoptera: Braconidae) in America north of Mexico. Journal of the Kansas Entomological Society 68: 245-262.
Whitfield JB (1997) Subfamily Microgastrinae. In Wharton RA, Marsh PM, Sharkey MJ (Eds) Manual of the New World genera of the family Braconidae (Hymenoptera). Special Publication No. 1, International Society of Hymenopterists, Washington, D.C., 333-364.
Whitfield JB (2006) Revision of the Nearctic Species of the Genus Pholetesor Mason (Hymenoptera: Braconidae). Zootaxa 1144: 1-94.
Whitfield JB, Mardulyn P, Austin AD, Dowton M (2002) Phylogenetic relationships among microgastrine braconid wasp genera based on data from the $16 \mathrm{~S}, \mathrm{COI}$ and 28 S genes and morphology. Systematic Entomology 27: 337-359.
Whitfield JB, Rodriguez JJ, Masonick PK (2009) Reared microgastrine wasps (Hymenoptera: Braconidae) from Yanayacu Biological Station and environs (Napo Province, Ecuador): diversity and host specialization. Journal of Insect Science 9 (27): 1-22.
Whitfield JB, Rasmussen C, Arias-Penna DC (in press). Review of the New World genus Venanus (Hymenoptera: Braconidae: Microgastrinae), with a new key and descriptions of three new reared Neotropical species. Annals of the Entomological Society of America.
Williams D (1985) The New World genus Lathrapanteles n.gen.: Phylogeny and placement in the Microgastrinae (Hymenoptera: Braconidae: Cotesini). Canadian Journal of Zoology 63: 1962-1981.
Williams D (1988) Classification, phylogeny and zoogeographic studies of species of Sathon Mason (Hymenoptera: Braconidae). Quaestiones Entomologicae 24: 529-638.
Williamson GD (1963) Summary of parasite and predator liberations in Canada and of insect shipments from Canada in 1963. Canadian Insect Pest Review 41:137-151.
Yu D, van Achterberg K, Horstmann K (2005) World Ichneumonoidea 2004. Taxonomy, Biology, Morphology and Distribution. CD/DVD. Taxapad, Vancouver, Canada.

## Appendix I.

Comprehensive data for type material of Microgastrinae described in this paper where DNA barcodes were obtained. The Sample ID and Process ID fields allow to retrieve all molecular and collection information for every specimen through BOLD (http:// www.barcodinglife.org). File format: Microsoft Excel (1997-2003). doi: 10.3897/ zookeys.63.565-app.I

## Appendix II.

Comprehensive data for all specimens of genera Cotesia and Diolcogaster where DNA barcodes were obtained. The Sample ID and Process ID fields allow to retrieve all molecular and collection information for every specimen through BOLD (http:// www.barcodinglife.org). File format: Microsoft Excel (1997-2003). doi: 10.3897/ zookeys.63.565-app.II

## Appendix III.

Comprehensive data for all specimens of genus Microplitis where DNA barcodes were obtained. The Sample ID and Process ID fields allow to retrieve all molecular and collection information for every specimen through BOLD (http://www. barcodinglife.org). File format: Microsoft Excel (1997-2003). doi: 10.3897/ zookeys.63.565-app.III

# A new herrerasaurid (Dinosauria, Saurischia) from the Upper Triassic Ischigualasto Formation of northwestern Argentina 

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#### Abstract

Herrerasauridae comprises a basal clade of dinosaurs best known from the Upper Triassic of Argentina and Brazil, which have yielded remains of Herrerasaurus ischigualastensis and Staurikosaurus pricei, respectively. Systematic opinion regarding the position of Herrerasauridae at the base of Dinosauria has varied. Here we describe a new herrerasaurid, Sanjuansaurus gordilloi gen. n., sp. n., based on a partial skeleton from Carnian-age strata of the the Upper Triassic Ischigualasto Formation of northwestern Argentina. The new taxon is diagnosed by numerous features, including long, band-shaped and posterolaterally oriented transverse process on the posterior cervical vertebrae; neural spines of the sixth to eighth dorsal vertebrae, at least, bearing acute anterior and posterior processes; scapula and coracoid with everted lateral margins of the glenoid; and short pubis ( $63 \%$ of the femoral length). Phylogenetic analysis placed Sanjuansaurus within a monophyletic Herrerasauridae, at the base of Theropoda and including Herrerasaurus and Staurikosaurus. The presence of Sanjuansaurus at the base of the Ischigualasto Formation, along with other dinosaurs such as Herrerasaurus, Eoraptor, Panphagia, and Chromogisaurus suggests that saurischian dinosaurs in southwestern Pangea were already widely diversified by the late Carnian rather than increasing in diversity across the Carnian-Norian boundary.


## Keywords

Dinosauria, Saurischia, Herrerasauridae, Carnian, Ischigualasto

## Introduction

Herrerasauridae (Benedetto 1973) is a clade of basal saurischian dinosaurs best known from the Upper Triassic of Argentina and Brazil (Reig 1963; Colbert 1970; Sereno and Novas 1992). Their phylogenetic position has varied in recent analyses from a position as sister-group of Dinosauria (Gauthier 1986; Brinkman and Sues 1987; Benton 1990; Novas 1992; Fraser et al. 2002), basal theropods (Sereno and Novas 1992; Sereno 1994, 1999; Sereno et al. 1993; Novas 1994, 1996, 1997; Rauhut 2003; Ezcurra and Cuny 2007; Ezcurra and Novas 2007; Bittencourt and Kellner 2009), or sister-group of Theropoda + Sauropodomorpha (Padian and May 1993; Bonaparte and Pumares 1995; Holtz 1995; Langer et al. 1999; Galton 2000; Langer 2004; Benton 2006; Ezcurra 2006; Irmis et al. 2007; Smith et al. 2007; Martinez and Alcober 2009). Resolving the phylogenetic position of Herrerasauridae is hindered by incomplete specimens and differences in character selection and scoring between analyses.

The close relationship between its two best known genera, Herrerasaurus and Staurikosaurus is well supported by a suite of synapomorphies (Novas 1994, 1996, 1997; Sereno and Novas 1994; Sereno 1999; Kellner and Campos 2000; Rauhut 2003; Langer 2004; Langer and Benton 2006; Bittencourt and Kellner 2009). Chindesaurus bryansmalli from the Norian Chinle Formation of the southwestern United States (Long and Murry 1995) has also been identified as a herrerasaurid (Long and Murry 1995; Novas 1997; Sereno 1999; Nesbitt et al. 2009) or as a more basal taxon (Langer 2004; Nesbitt et al. 2007; Bittencourt and Kellner 2009).

Here we describe a new herrerasaurid from strata near the basal contact of the Ischigualasto Formation. The new taxon is based on an associated, partially articulated skeleton recovered from Ischigualasto Provincial Park in 1994.

## Geological and palaeontological settings

The holotype of the new taxon (PVSJ 605) was found in 1994 during fieldwork carried out by the Instituto y Museo de Ciencias Naturales of the Universidad Nacional de San Juan. The Ischigualasto Formation crops out in northwestern Argentina and forms part of the Ischigualasto-Villa Unión Basin (Figure 1). It reaches up to 700 m in thickness and comprises fluvial channel sandstones with sandstones and mudstones deposited on a well-drained floodplain. Interlayered volcanic ashes 20 m above the base of the formation provide chronostratigraphic control and have yielded an age of 231.4 Ma , placing them in the Carnian stage (Rogers et al. 1993; Renne et al. 2010).

The Ischigualasto Formation is divided into four members (Currie et al. 2009). From the base to the top they are: the La Peńa (from the base to 40 m ), the Cancha de Bochas ( 40 to 180 m ), the Valle de la Luna ( 180 to 650 m ) and the Quebrada de la Sal ( 650 to 700 m ) members (Figure 1). The La Peńa Member consists of multi-story channel sandstones and conglomerates covered by poorly-drained floodplain mudstones. The Cancha de Bochas Member is composed of thick, well-drained floodplain


Figure I. Geological map of the Ischigualasto - Villa Unión Basin (northwestern Argentina) and section of the Ischigualasto Formation at the type locality. The red star indicates the site of the holotype of Sanjuansaurus gordilloi (PVSJ 605), near the base of the Ischigualasto Formation.
mudstones interbedded with high-sinuosity channel sandstones. The Valle de la Luna Member is mostly characterized by amalgamated high-sinuosity channels, abandoned channels and marsh deposits. Finally, the Quebrada de la Sal Member consists of tabular fluvial deposits.

The new fossil was excavated at the La Gallinita locality, which is located in the lowest levels of the Cancha de Bochas Member. It was found 40 m above the base of the formation. Dinosaurs, including several specimens of Herrerasaurus ischigualastensis and Eoraptor lunensis, the holotype of Panphagia protos, and other as yet undescribed species (Martinez et al. 2008), carnivorous and herbivorous cynodonts, rhynchosaurs, and crurotarsan archosaurs were recovered from the same level.

## Methods

## Preservation and preparation

The reddish brown bones were covered by a coarse hematite crust, and the entire specimen was embedded in a grey-green, fine-grained sandstone matrix. The overall preservation of the specimen is good. All the bones are three-dimensionally preserved, and most are complete with the exception of the femora, which are partially distorted and lack fine details. The incompleteness of the skeleton is attributable to pre-burial processes, although the third, fourth and anterior part of the fifth dorsal vertebra were lost in the course of preparation. The specimen was prepared using a pneumatic air scribe and pin vice.

## Terminology

We employ traditional, or "Romerian," anatomical and directional terms rather than their veterinarian alternatives (Wilson 2006). "Anterior" and "posterior", for example, are used as directional terms rather than "rostral" or "cranial" and "caudal". We also follow Wilson's (1999) recommendations regarding the identification of vertebral laminae in saurischians.

We used the stem-based phylogenetic definition for Herrerasauridae proposed by Sereno (Sereno 2005) rather than the node-based definition (Sereno and Novas 1992, Langer 2004), obviating the need for a suprafamilial taxon (Herrerasauria; Langer 2004). We thus define Herrerasauridae as "the most inclusive clade containing Herrerasaurus ischigualastensis but not Passer domesticus"(Sereno 2005).

## Phylogenetic Analysis

In order to asses the phylogenetic position of the new taxon among basal Dinosauria, we added it (Table 1) and the recently described basal sauropodomorph Panphagia (Martinez and Alcober 2009) to the character-taxon matrix published by Langer and Benton (2006). We also modified several character states for these basal taxa following Martínez and Alcober (2009). The software used to analyze the phylogenetic relationships was TNT 1.1 (Goloboff et al. 2003).

## Nomenclatural Acts

This published work and the nomenclatural acts it contains have been registered in ZooBank, the proposed online registration system for the ICZN. The ZooBank LSIDs (Life Science Identifiers) can be resolved and the associated information viewed through any standard web browser by appending the LSID to the prefix "http://zoo-

Table I. Character state scores for Sanjuansaurus gordilloi (PVSJ 605). Data lines inserted into the data matrix of Langer and Benton [33] with the addition of Martinez and Alcober [30]

| Sanjuansaurus | $0 ? ? ? ? ? 00 ? ? ~ ? ? ? ? ? ~ ? ? ? ? ? ~ ? ? 000 ~$ |
| :--- | :--- |

bank.org/". The LSID for this publication is: urn:lsid:zoobank.org:pub:FB2AE660-C3EE-4348-BF9F-F4311C47E853.

## Institutional abbreviations:

PVSJ Instituto y Museo de Ciencias Naturales, San Juan 5400, Argentina.

## Results

## Systematic Paleontology

## Systematic hierarchy

Dinosauria Owen, 1842<br>Saurischia Seeley, 1887<br>Herrerasauridae Benedetto, 1973

## Sanjuansaurus gen. n. <br> urn:lsid:zoobank.org:act:DC75ADA0-0C6B-41D5-8E29-CD76725FD704

Etymology: Sanjuan, in reference to San Juan Province, Argentina; saurus, lizard (Latin).
Type species: Sanjuansaurus gordilloi

## Sanjuansaurus gordilloi sp. n.

urn:lsid:zoobank.org:act:84F081D6-4E0A-414E-83A3-D994263C1005

Etymology: gordilloi, in honor of Raul Gordillo, head fossil preparator and artist in the laboratory of the San Juan Museum and team member during many years of excavation.

Holotype: PVSJ 605, an incomplete skeleton including left maxilla, partial axial column, from the axis to the twelfth caudal vertebra, lacking the third, fourth, and anterior half of the fifth dorsal vertebrae, both scapulae, left ulna, ungual phalanx of left? digit III, preacetabular portion of the left ilium, proximal end of left and complete
right pubis, both femora and tibiae, right fibula, right astragalus and calcaneum, and left metatarsal II.

Type locality: The specimen was found in the Cancha de Bochas Member (Currie et al. 2009), 40 m above the base of Ischigualasto Formation. The type locality, informally called "Herrera de la base", is located 3 km northwestern of "Cancha de Bochas" locality, Ischigualasto Provincial Park, San Juan, Argentina (Figure 1).

Horizon and age: 40 m above the base of the Ischigualasto Formation, Late Triassic, Carnian (ca. 231.4 Ma), Ischigualasto-Villa Unión Basin (Rogers et al. 1993; Renne et al. 2010). The type horizon lies at approximately the same level as the dated ash, which implies a late Carnian age for the specimen.

Diagnosis: Diagnosed by the following autapomorphies: shelf-like, posterolaterally directed transverse processes on the posterior cervical vertebrae; neural spines of the sixth to eighth dorsal vertebrae, at least, bearing acute anterior and posterior processes; everted lateral margins of the glenoid; short pubis ( $63 \%$ of the femoral length); and pronounced, rugose scar on the medial surface of the femur at the level of the fourth trochanter.

These features distinguish Sanjuansaurus gordilloi from the previously described herrerasaurids, such as Herrerasaurus ischigualastensis and Staurikosaurus pricei, as well as other basal saurischians from Ischigualasto Formation, such as Eoraptor lunensis (Sereno et al. 1993), Panphagia protos (Martinez and Alcober 2009), and Chromogisaurus novasi (Ezcurra 2008, 2010)

## Description

Although some bones of Sanjuansaurus gordilloi were disarticulated, the proximity of all elements, found in an area of only one square meter, their complementary size, and the absence of any duplicated elements suggest that they represent a single individual (Figure 2). In size and general proportions (Table 2, 3), the new specimen (Figure 3A) is comparable to a medium-sized Herrerasaurus (Figure 3B), and slightly larger than the only known specimen of Staurikosaurus (Figure 3C).

Cranium. The left maxilla is the only cranial bone preserved (Figure 4A). It exhibits the anteroposteriorly elongated dorsal process and transversely narrow antorbital fossa as in Herrerasaurus (Figure 4B, C) but unlike the wide fossa of Eoraptor (Sereno et al. 1993: Fig. 2A). The anterodorsal border of the antorbital fossa shows a slit-shaped promaxillary fenestra as in Herrerasaurus, some coelophysoids, Zupaysaurus, and most tetanurans (Welles 1984; Witmer 1997; Arcucci and Coria 2003; Sereno 2007). The anterior border of the maxilla is slightly convex and preserves the posterior border of the subnarial foramen as in other saurischians. Breakage of the dorsal portion makes it impossible to determine whether there is an oval fenestra between the premaxilla and maxilla as in Herrerasaurus (Sereno and Novas 1994). The dorsal border of the jugal process below the antorbital fenestra is horizontal (Figure 4). In specimens of Herrerasaurus, this suture is either horizontal (PVSJ 053, holotype of "Frenguellisaurus ischigualastensis") or posteroventrally inclined (PVSJ 407) (Sereno and Novas 1994: Fig. 1).


Figure 2. Preserved bones of Sanjuansaurus gordilloi (PVSJ 605), positioned as they were found in the field. Abbreviations: cal-I5, caudal vertebrae 1-15; c2-9, cervical vertebrae 2-9; dI-I4, dorsal vertebrae 1-14; I Fe, left femur; I il, left ilium; I MII, left metatarsal II; ISc, left scapula and coracoid; ITi, left tibia; $\boldsymbol{I}$ UI, left ulna; $\mathbf{P h}$, manual phalanx; $\boldsymbol{R}$, rib; $\boldsymbol{r} \boldsymbol{A s} \mathbf{- C a}$, right astragalus and calcaneum; $\boldsymbol{r} \boldsymbol{F e}$, right femur; $\boldsymbol{r}$ Fi, right fibula; $\boldsymbol{r} \mathbf{F e}$, right femur; $\boldsymbol{r} \mathbf{M x}$, right maxilla; $\boldsymbol{r} \mathbf{P u}$, right pubis; $\boldsymbol{r} \mathbf{S c}$, right scapula and coracoid; $\mathbf{r T i}$, right tibia; $\mathbf{s} \mathbf{I} \mathbf{- 3}$, sacral vertebrae $1-3$. Scale bars equals 20 cm .

Axial skeleton. The cervical vertebrae are preserved from the incomplete atlas to the last vertebra of the series (Figure 5A, B). Sanjuansaurus has nine cervical vertebrae. The last cervical vertebra differs from the first dorsal vertebra in the presence of a ventral keel and being nearly $30 \%$ longer, with the paraphophysis being more anteriorly located and the capitulum of the associated rib being more slender (Figure 2, 3, 5A). Although ten cervical vertebrae have been reported in Herrerasaurus (Sereno and Novas 1994), the cervicodorsal transition is not well preserved on any of the known specimens.

The atlas is represented only by its centrum, the odontoid (Figure 5A), which is completely co-ossified with the axial centrum. It is subcircular in dorsal view with a pointed median projection as in Herrerasaurus (Sereno and Novas 1994). It is semilunar in outline in anterior view. The dorsal and ventral surfaces are concave and convex, respectively, as in Herrerasaurus.

The axial intercentrum (Figure 5A) is fused to the axial centrum. It is much broader than the anterior end of the axial centrum as in Herrerasaurus. In lateral view it is subquadrangular rather than triangular as in Herrerasaurus (Sereno and Novas 1994). Its anteroposterior length is one-half that of the axis, resembling that in large specimens of Herrerasaurus (PVSJ 053), but proportionately longer than that in the small ones (e.g,

Table 2. Dimensions (mm) of preserved vertebrae (Figures 2, 3, 5) from the holotypic specimen of Sanjuansaurus gordilloi (PVSJ 605).

| Vertebra | Centrum_length $^{\mathbf{1}}$ | Vertebra | Centrum_length $^{\mathbf{1}}$ |
| :--- | :---: | :--- | :---: |
| C2 | 37.0 | D13 | 36.0 |
| C3 | 42.5 | D14 | 34.5 |
| C4 | 44.0 | S1 | 38.0 |
| C5 | 46.1 | S2 | 48.0 |
| C6 | 47.5 | S3 | 46.2 |
| C7 | 45.6 | CA1 | 35.8 |
| C8 | 38.5 | CA2 | 36.8 |
| C9 | 38.0 | CA3 | 35.0 |
| D1 | 33.6 | CA4 | 37.0 |
| D2 | 28.3 | CA5 | 33.2 |
| D6 | 36.8 | CA6 | 32.3 |
| D7 | 38.0 | CA7 | 38.5 |
| D8 | 38.8 | CA8 | 38.5 |
| D9 | 36.6 | CA9 | 37.8 |
| D10 | 37.7 | CA10 | 37.8 |
| D11 | 37.5 | CA11 | 36.5 |
| D12 | 38.0 |  |  |

Abbreviations: C cervical; CA caudal; D dorsal; S sacral.
${ }^{1}$ Measured along ventral edge excluding anterior convexity of centrum when present.

PVSJ 407), where it equals one-third of axial centrum length. As in Herrerasaurus the axial intercentrum is deeply cupped anteriorly.

The axial centrum (Figure 5A) is twice as long as it is deep and bears a pronounced ventral keel as in Herrerasaurus (Sereno and Novas 1994). The diapophyses are short and face dorsolaterally as in Herrerasaurus, although they are located more anteriorly and are level with the axial intercentrum. In Herrerasaurus the diapophyses do not extend beyond the anterior articular surface of the centrum. Damage to the neural spine and the postzygapophyses preclude description of their structure.

The postaxial cervical centra are spool-shaped, amphicoelous, and have pronounced ventral keels. In Herrerasaurus, by contrast, the lateral and ventral sides of the centrum are less concave, and the ventral keel diminishes progressively in more distal vertebrae (Sereno and Novas 1994). The second to the sixth cervical centra are approximately parallelogram-shaped in lateral view whereas the seventh to the ninth centra are subrectangular. The third cervical vertebra is longer than the axis, and centrum length increases posteriorly up to the sixth cervical centrum (Figure 5A) as in Herrerasaurus (Sereno and Novas 1994). This condition is different from Staurikosaurus, in which the third or fourth centrum is the longest (Galton 1977; Bittencourt and Kellner 2009). The parapophyses of the anterior cervical vertebrae of Sanjuansaurus protrude ventrally beyond the ventral margin of the centrum in lateral view, in contrast to the condition

Table 3. Dimensions (mm) of girdle and limb bones (Figures 2, 3, 6-8) of the holotypic specimen of Sanjuansaurus gordilloi (PVSJ 605).

| Bone |  |  |
| :--- | :--- | :---: |
| Scapulocoracoid | Coracoid, maximum height | Length |
|  | Posterior process (glenoid to tip of process) | 63.0 |
|  | Scapular length | 131.0 |
|  | Scapular blade, minimum width | 185.0 |
|  | Scapular blade, distal width | 18.5 |
|  | Height (glenoid to acromion) | 26.8 |
| Ulna | Maximum length | 89.5 |
|  | Anteroposterior shaft diameter (mid-shaft) | 178.2 |
|  | Length (acetabulum to foot) | 10.1 |
|  | Iliac peduncle length | 260.0 |
|  | Ischial peduncle length | 32.0 |
|  | Pubic foot, maximum length | 29.0 |
|  | Pubic foot, maximum width | 100.2 |
| Femur | Maximum length | 21.5 |
|  | Maximun distal width | 395.0 |
|  | Length | 20.5 |
|  | Maximun proximal dimension | 91.0 |
|  | Proximal width | 41.5 |
|  | Distal transverse width | 40.0 |
|  | Distal anteroposterior width | 43.5 |
| Astragalus-Calcaneum | Proximodistal depth | Transverse width |
|  | Medial anteroposterior width | 83.0 |
|  | Length | 37.5 |
|  | Maximun proximal dimension | 147.5 |
|  | Distal transverse width | 40.0 |
|  |  | 32.0 |

in Herrerasaurus, where they are located slightly dorsal to the ventral border of the centrum. Posteriorly, from the seventh vertebra, the parapophyses are displaced progressively backwards and upwards. All the cervical neural spines are broken at their bases. From the third to the ninth vertebra, the prezygapophyses extend one third of the centrum length beyond the anterior border of the body. The postzygapophyses are high and do not project behind the level of the posterior face of the centrum. As in Herrerasaurus (Sereno and Novas 1994), the epipophyses are pointed and extend beyond the postzygapophyses (Figure 5A). On the sixth cervical vertebra, anterior and posterior centrodiapophyseal, postzygodiapophyseal, and prezygodiapophyseal laminae are present and become more prominent on successive cervical vertebrae. From the fifth cervical vertebra onwards, the transverse processes increase in both anteroposterior width and transverse length and project posteroventrolaterally (Figure 5B), an unusual shape


Figure 3. Silhouette reconstruction of the skeletons of the best known herrerasaurids. Sanjuansaurus gordilloi (PVSJ 605) (A) Herrerasaurus ischigualastensis (B) Staurikosaurus pricei (C) Scale bars equals 20 cm . A: missing bones of Sanjuansaurus modified from Sereno, 1994; B: from Sereno, 1994; C: from Novas, 1997.
among theropods. The transverse processes are triangular in Herrerasaurus (Sereno and Novas 1994) and Staurikosaurus (Galton 1977).

The dorsal vertebrae are articulated. Only the third, fourth and anterior half of the fifth vertebra are lacking and were accidentally lost during preparation (Figure 5A-C). Thus we can say with confidence that there are 14 dorsal vertebrae as in Herrerasaurus (Sereno 2007, contra Novas 1994), in contrast to 15 in Staurikosaurus (Galton 1977; Bittencourt and Kellner 2009). The dorsal vertebrae are characterized by anteroposteriorly short centra and tall neural arches as in Herrerasaurus and Staurikosaurus (Novas 1994; Colbert 1970; Bittencourt and Kellner 2009). They differ in having more distinctly spool-shaped centra (Figure 5C). The ventral concavity is very conspicuous in the first to eleventh dorsal vertebrae, decreasing slightly in the twelfth


Figure 4. Maxilla of Sanjuansaurus gordilloi (PVSJ 605). Left maxilla of Sanjuansaurus in lateral view (A) Skull of Herrerasaurus (PVSJ 407) in left lateral view (B) Left maxilla of Herrerasaurus (PVSJ 053) in lateral view (C) Abbreviations: af, antorbital fossa; dp, dorsal process; ip, internarial process; J, jugal; jp, jugal process; $\boldsymbol{M}$, maxilla; of, oval fenestra; $\mathbf{p f}$, promaxillary fenestra; $\mathbf{P O}$, postorbital. Scale bars equals 5 cm .
to fifteenth. Centrum length decreases from the first to the second dorsal, increases from the sixth to the twelfth, and decreases again to the final dorsal vertebra (Table 2). A ventral keel is absent on all dorsal vertebrae although a prominent keel is present on the last cervical vertebra. The parapophyses are prominent and oval in lateral view. On the first and second dorsals, they are located at mid-length of the centrum. In more posterior dorsal vertebrae, they are displaced anterodorsally. On the twelfth dorsal vertebra, the parapophyses and diapophyses are located at the same level. The parapophyses of the first and second dorsal vertebrae are shared between the centrum and neural arch. In the sixth vertebra (the first completely preserved vertebra posterior to the second), the parapophyses are located entirely on the neural arch (Figure


Figure 5. Axial skeleton of Sanjuansaurus gordilloi (PVSJ 605). Nine anterior cervical and two anterior dorsal vertebrae in left lateral view (A). Cervical vertebrae 7, 8 and 9 in left lateral view (B). Dorsal vertebra 1 to caudal vertebra 1 in left lateral view $(\mathbf{C})$. Reconstruction of the sacrum in left lateral view (D). Caudal vertebra 1 to 12 in left lateral view (E). Abbreviations: acdl, anterior centrodiapophyseal lamina; $\boldsymbol{a i}$, axis intercentrum; $\boldsymbol{a p}$, anterior process of dorsal neural spine; $\boldsymbol{c a l} \mathbf{I} \mathbf{I 2}$, caudal vertebrae 1 to $12 ; \mathbf{c 2 - 9}$, cervical vertebrae 2 to 9 ; $\mathbf{d}$, diapophysis; $\boldsymbol{d} \mathbf{I} \mathbf{- I 3}$, dorsal vertebrae 1 to 13 ; $\mathbf{e p}$, epipophysis; ns, neural spine; od, odontoides; $\mathbf{p}$, parapophysis; $\mathbf{p c \boldsymbol { d }}$, posterior centrodiapophyseal lamina; prz, prezygapophysis; poz, postzygapophysis; $\mathbf{p p}$, posterior process of dorsal neural spine; $\boldsymbol{s} \boldsymbol{I} \mathbf{- 3}$, sacral vertebrae 1 to 3 ; $\boldsymbol{s r l} \mathbf{I} \mathbf{3}$, sacral ribs 1 to 3; st, spine table; $\boldsymbol{t}$, tooth; $\mathbf{t p}$, transverse process; $\mathbf{v k}$, ventral keel. Scale bar equals 5 cm .

5B). The neural arches are anteroposteriorly short and dorsoventrally deep. Pre- and postzygapophyses are anteroposteriorly short, the former are slightly longer than the latter and extend beyond the anterior centrum face as in Herrerasaurus (Novas 1994). Pre- and postzygapophyses are separated by an interzygapohpyseal sulcus, which extends onto the anterior and posterior edges of the neural spine as in Herrerasaurus and Staurikosaurus (Novas 1994; Bittencourt and Kellner 2009). The second dorsal vertebra, which is disarticulated from the posterior part of the vertebral column, has a well developed hyposphene similar to that present in Herrerasaurus (Novas 1994). The remaining dorsals presumably also had hyposphene-hypantrum articulations, but these are obscured by the tight articulation between vertebrae. The anterior neural spines are broken off with the exception of those on the sixth and eighth dorsal vertebrae. These have distinctive pointed processes extending anteriorly and posteriorly from the apex of the spine (Figure 5C, D). The distal end of the neural spine of the last dorsal vertebrae also bears a spine table, which is similar to that in Herrerasaurus (Novas 1994). All the dorsal vertebrae have well developed anterior and posterior centrodiapophyseal, postzygodiapophyseal, and prezygodiapophyseal laminae. These
laminae bound three subtriangular spaces the infraprezygapophyseal, infradiapophyseal and infrapostzygapophyseal fossae (Figure 5C). These fossae converge below a horizontal roof formed by the diapophysis and pre- and postzygodiapophyseal laminae as in Herrerasaurus.

The sacrum (Figure 5C, D) of Sanjuansaurus comprises three vertebrae. The first is a dorsosacral whereas the second and third represent the primordial sacral pair as in Herrerasaurus (Sereno 2007, contra Novas 1994). In Staurikosaurus the sacrum is composed of two primordial sacrals, with some uncertainty concerning the presence of a dorsosacral or caudosacral (Bittencourt and Kellner 2009). Given the degree of neurocentral coossification in other parts of the axial column and the fusion of the sacral ribs to their respective centra, it is surprising that the sacral centra are not co-ossified.

The first sacral vertebra is $10 \%$ longer than the last dorsal vertebra, and the position of the infradiapophyseal laminae and the transverse processes are somewhat different. The posterior centrodiapophyseal lamina is displaced anteriorly toward the anterior centrodiapophyseal lamina, so that ventral to the transverse process they both extend nearly vertically (Figure 5C, D). The transverse process is not a single flat process as on the posterior dorsal vertebrae but rather is composed of two laminae, one horizontal and the other one vertical, which join to form an inverted L-shape near the contact with the ilium. This configuration is similar to that shown on dorsal vertebra 15 in Herrerasaurus (Novas 1994: Fig. 1). The addition of the ventral lamina presumably strengthened the transverse process. The latter expands posterolaterally toward its distal end, which is broken away. The form of the process and its distal expansion suggest that it probably contacted the preacetabular process of the ilium, but this contact or the distal articular surface is not preserved. The distal end of the neural spine is expanded to form a spine table as in Herrerasaurus (Novas 1994). The anterior and posterior borders of the neural spine have median sulci that extend between the preand postzygapophyses, respectively.

The second sacral vertebra is $25 \%$ longer than the first and is the longest in the sacrum (Figure 5C, D). This is true for one individual of Herrerasaurus (PVSJ 373), whereas in another (PVL 2566) the third sacral vertebra is longest (Novas 1994). The centrum is transversally narrower and dorsoventrally flatter, and the neural spine is broader than in the first sacral vertebrae as in Herrerasaurus (Novas 1994). The spine table and anterior and posterior median sulci are twice the transverse width of the corresponding features on the first and third sacral vertebrae. The ribs are extensively fused to the anterodorsal portion of the centrum.

The third sacral vertebra, the most robust of the sacrum, is dorsolaterally flattened and transversally expanded as in Herrerasaurus (Novas 1994) (Figure 5C, D). As on the second sacral vertebra, robust sacral ribs are fused to the centrum. The ventral border of the rib is located at the same level as the ventral surface of the centrum, in contrast to the condition in Herrerasaurus, in which the rib is offset dorsally (Novas 1994). The neural spine is equal in height to the second sacral but is lateromedially narrower.

The sacral ribs of the second and third sacral vertebrae have broad distal attachment surfaces that are continuous and, in lateral view (Figure 5D) form a C-shape that opens dorsally. Large subcircular openings are present between the articular ends of the sacral ribs and the centra as in Herrerasaurus (Novas 1994).

The first 15 caudal vertebrae of PVSJ 605 are preserved in articulation. The posterior end of the fifteenth vertebra and all the hemal arches are lacking (Figure 5E). The preserved centra are strongly constricted, or spool-shaped, more so than in Herrerasaurus (Novas 1994: Fig. 4). As in Herrerasaurus and Staurikosaurus (Bittencourt and Kellner 2009), the centra lack ventral keels. The first caudal centrum is $10 \%$ shorter than that of the last sacral, and this length is maintained with minor variation along the preserved series, despite the decreasing height of the centra (Table 2). The neural arches are very tall with zygapophyses located far from the transverse process as in Herrerasaurus (Novas 1994). The subhorizontal transverse processes are situated in the middle of the centrum and project laterally and slightly posteriorly. In section the transverse processes are dorsoventrally flattened, in contrast to the semicircular section evident in Herrerasaurus (Novas 1994) and Staurikosaurus (Bittencourt and Kellner 2009). The only preserved neural spines, the third and fourth, are tall and near vertical, as is the case with the proximal caudal spines in Herrerasaurus. The caudal neural spines lack the anterior and posterior sulci present on the dorsal and sacral spines, and on the anterior caudals of Herrerasaurus (Novas 1994). The prezygapophyses extend beyond the anterior centrum face, whereas the postzygapophyses terminate flush with the posterior centrum face.

Appendicular Skeleton. Each scapula is firmly fused to its respective coracoid. The anterior margin is broken away on both scapulae, although its curved margin can be restored. The acromial process diverges from the blade at an angle slightly greater than $90^{\circ}$, as in Herrerasaurus (Sereno 1994). The glenoid is shared unevenly between the scapula and coracoid, the former contributing a smaller portion of the articulation, as in Herrerasaurus. The margin, or lip, of the glenoid protrudes laterally in a conspicuous manner, which does not seem to be an artifact of preservation (Figure 6A). The scapular blade is straplike with narrow proportions in lateral view (Figure 6A, B). The minimum width of the blade (near the base) is $54 \%$ the width of the acromial margin. This ratio is smaller than that found in either small ( $83 \%$; PVSJ 407) or very large individuals (60\%; PVSJ 053, "Frenguellisaurus") of Herrerasaurus. The dorsal margin of the acromion is thin in contrast to the thickened border in Herrerasaurus (Sereno 1994). The lateral surface of the scapular blade has a distinct crest along the proximal two thirds of its length as in Herrerasaurus (Sereno 1994). In lateral view the blade is gently arched posteriorly in contrast to the nearly straight blade in Herrerasaurus.

The semicircular, plate-shaped coracoid (Figure 6A, B) is broader anteroposteriorly than dorsoventrally as in Herrerasaurus (Sereno 1994). It is gently concave medially. As in Herrerasaurus, the coracoid foramen is located anteroventral to the glenoid, opening anterolaterally entirely within the coracoid. The margin of the glenoid is particularly prominent laterally, forming a shelf (Figure 6A). The hook-shaped posteroventral pro-


Figure 6. Preserved shoulder blade and forelimb bones of Sanjuansaurus gordilloi (PVSJ 605). Left scapula and coracoid in posterior $(\mathbf{A})$, and lateral $(\mathbf{B})$ views. Left ulna in lateral $(\mathbf{C})$, medial $(\mathbf{D})$, and anterior views (E). Ungual phalanx of digit III in proximal $(\boldsymbol{F})$ and lateral view $(\boldsymbol{G})$. Abbreviations: ac, acromion; $\boldsymbol{a r}$, anterior ridge; $\boldsymbol{C}$, coracoid; $\mathbf{c g}$, collateral groove; $\mathbf{C f}$, coracoid foramen; $\mathbf{C l}$, coracoid lip; $\mathbf{g}$, glenoid surface; Haf, humeral articular facet; Ic, lateral crest; Ip, lateral prominence; Ir, lateral ridge; Is, ligament scars; $\boldsymbol{I} \boldsymbol{p}$, lateral prominence; ol, olecranon ; ovd, oval depression; $\boldsymbol{p} \boldsymbol{v p}$, posteroventral process; Raf, radius articular facet; S, scapula; SI, scapular lip; Uaf, ulnare articular facet. Scale bar equals 5 cm .
cess of the coracoid is long and pointed (Figure 6B), similar to that in ornithomimids such as Gallimimus (Osmólska and Barsbold 1990: Fig. 4). When the scapular blade is held vertically it is seen to extend far posterior to the glenoid. The process is considerably shorter in Herrerasaurus (Brinkman and Sues 1987: Fig. 2-10). The glenoid is separated from the posteroventral process by a notch marked by a deep depression (Figure 6A).

The ulna is more gracile than that of Herrerasaurus (Sereno 1994), but otherwise similar in shape. The proximal end bears a prominent olecranon process and a concave articular surface (Figure 6C-E). The lateral surface of the proximal end has a distinct protuberance that contributes to a concave articular surface for the proximal end of the radius as in Herrerasaurus (Sereno 1994). In Sanjuansaurus the ulnar protuberance is more acute. The medial surface of the proximal end is slightly concave, in contrast to the convex surface of Herrerasaurus, although this difference may be due to postmortem deformation in Sanjuansaurus. The distal half of the ulnar shaft shows a gentle medial curvature and has longitudinal ridges on its anterior, lateral and medial surfaces as in Herrerasaurus (Sereno 1994). The ulnar shaft of Sanjuansaurus appears to be more slender than in Herrerasaurus. The distal end of the ulna exhibits several differences to that of Herrerasaurus. It is expanded to a lesser degree than in small individuals of Her-
rerasaurus (e.g, PVSJ 373; Sereno 1994). The articular surface for the ulnare is concave and faces anteromedially (Figure 6D, E) in contrast to the convex surface of Herrerasaurus. Anterolateral to this articular facet, there is a protuberance that extends distally (Figure 6C-E). This protuberance may be homologous with a subtriangular ligament rugosity in Herrerasaurus (Sereno 1994).

Of the manus only one manual ungual (Figure 6F, G) is preserved. The ungual has been crushed transversely. Its curvature and transversely narrow proportions (Figure 6 F) identify it as pertaining the the manus rather than the pes. Its small size, short and deep proportions, and ventral position of the attachment groove suggest that it is probably the fourth (terminal) phalanx of the third digit. The ungual has a well developed flexor tubercle more deeply grooved on the left side (Figure 6G). Although we considered that it is the smaller ungual of the hand, it is still small compared to individuals of Herrerasaurus (PVSJ 373) smaller in overall size than Sanjuansaurus.

A fragment of the left ilium comprises the distal portion of the pubic peduncle (Figure 7D). It is fused with the proximal end of the pubis, and preserved in articulation with the left femur (although the latter is dorsally rotated from its natural position). Medially it is also fused to a distal fragment of the second sacral rib. The pubic peduncle is stout, anteroventrally directed and forms the anterior border of a wide perforate acetabulum as in Herrerasaurus (Novas 1994). The supra-acetabular crest forms the straight lateral edge of the pubic peduncle, extending posterodorsally over the acetabulum as in Herrerasaurus.

The pubis is relatively short, its proximodistal length comprising only $63 \%$ the length of the femur (Figure 7A-C). By contrast, in Herrerasaurus and Staurikosaurus, the length of the pubis equals $91 \%$ (PVL 2566) and $70 \%$ the length of the femur, respectively. The two proximal articular surfaces are set at an angle of $130^{\circ}$. The first faces posteriorly and articulates with the ischium whereas the second faces posterodorsally and includes an acetabular section and an articular facet for the ilium. A marked prominence, more distinct than that seen in Herrerasaurus (Novas 1994), is located on the anterolateral margin of the pubis near the iliac peduncle and is presumed to represent the insertion site for the ambiens muscle. The oval obturator foramen is large, its anteroposterior diameter measuring $34 \%$ of the anteroposterior width of the proximal end. In Sanjuansaurus the pubis shaft lacks the strong proximal curvature characteristic of Herrerasaurus (Novas 1994), although the lateral margin of the shaft has a similar sinuous curvature in anterior view. The distal portion of the pubis expands and is turned posteriorly to form a pubic "foot" as in Herrerasaurus and Staurikosaurus (Novas 1994; Bittencourt and Kellner 2009). The anteroposterior width of the pubic "foot" is $40 \%$ of pubic length, which is slightly less than in Herrerasaurus ( $43 \%$ and $48 \%$ in small and large individuals, respectively) (Novas 1994), but greater than in Staurikosaurus (26\%).

Both femora are poorly preserved (Figure 7D-H). The left femur is complete and articulated with the ilium, although rotated dorsally from its natural articulation (Figure 7D). Only the proximal and distal ends of the right femur are preserved (Figure 7E). The femur is sigmoid in lateral and anterior views (Figure 7D, E). The


Figure 7. Pelvic and hind limb bones of Sanjuansaurus gordilloi (PVSJ 605). Right pubis in anterodorsal (A), lateral (B), and medial views (C). Left femur articulated with the preacetabular portion of the ilium and proximal end of the pubis in lateral view (D). Right femur in medial view (E). Right femur head in proximal view $(\mathbf{F})$. Proximal end of the right femur in anteromedial view $(\mathbf{G})$. Distal end of the left femur in distal view $(\mathbf{H})$. Left tibia in lateral ( $\mathbf{I}$ ), medial ( $\mathbf{J}$ ), anterior $(\mathbf{K})$, posterior $(\mathbf{L})$, proximal ( $\mathbf{M}$ ), and distal views $(\mathbf{N})$. Left metatarsal II in anterior view $(\mathbf{O})$. Distal end of the right tibia in posterior view ( $\mathbf{P}$ ). Abbreviations: aa, acetabular area; ao, abnormal outgrowth in posteroventral process; cc, cnemial crest; $\mathbf{c t f}$, crista tibiofibularis; $\mathbf{4 t}$, fourth trochanter; $\mathbf{f c}$, fibular condyle; $\boldsymbol{f h}$, femoral head; $\mathbf{g t}$, greater trochanter; Isaf, ischium articular facet; II, illium; Isaf, ischium articular facet; Ic, lateral condyle; mae, ambiens muscle eminence; $\boldsymbol{m} C F L \mathbf{s}$, scars for attachment of muscle caudifemoralis longus; of, obturator foramen; $\mathbf{p f}$, pubic foot; $\boldsymbol{p} \boldsymbol{v}$, posteroventral process; $\boldsymbol{r P}$, right pubis; sac, supraacetabular crest; $\boldsymbol{t c}$, tibial condyle; ts, trochanteric shelf. Scale bar equals 5 cm .
anteromedially projecting head lies at an angle of approximately $65^{\circ}$ to the transverse axis of the distal end. This is slightly more divergent than in Herrerasaurus ( $55^{\circ}$; Novas 1994). The size of the head is smaller and narrower transversally than in small individuals of Herrerasaurus (PVSJ 373) that are smaller in overall size than Sanjuansaurus. In proximal view the head is kidney-shaped (Figure 7F), and its proximal surface is smoothly convex as in Herrerasaurus (Novas 1994), although Sanjuansaurus lacks the facies articularis antitrochanterica present in the latter (Novas 1994). The anterior surface of the femoral neck lacks the pronounced anterior trochanter present in Herrerasaurus (Novas 1994). Although partially obscured by deformation
and adhering hematite, the trochanteric shelf is present on the lateral surface of the femur (Figure 7E). The shaft of the left femur appears to be more robust than that of Herrerasaurus, although this may be an artifact of preservation. Anteriorly, it has a pronounced keel that extends from the level of the trochanteric shelf proximally to the distal quarter of the femur. The fourth trochanter is semi-elliptical in lateral view and located on the proximal third of the femur (Figure 7E), similar to the condition in Chindesaurus (Long and Murry 1995: Fig. 184). It is longer (one fourth of femoral length), thinner, and seemingly more symmetrical than in Herrerasaurus. A very large, pronounced and rugose protuberance is present on the medial surface of the femur at the level of the fourth trochanter, presumably for the insertion of M. caudifemoralis longus (Figure 7G). In Herrerasaurus this protuberance is relatively small and smooth. The distal end of the femur is expanded. The anterior surface is convex transversally, lacks an intercondylar groove, and has a large attachment scar that extends laterally as in Herrerasaurus (Novas 1994). The posterior surface has a deeper popliteal fossa than in Herrerasaurus (Novas 1994). The crista tibiofibularis is separated by a sulcus from the fibular condyle and projects farther posteriorly than the tibial condyle (Figure 7 H ). The articular surface of the distal end has a concavity extending from the popliteal fossa medially to the groove between the crista tibiofibularis and the fibular condyle as in Herrerasaurus.

The left tibia of Sanjuansaurus is complete and well preserved (Figure 7I-N). The right tibia is preserved in articulation with the fibula. The distal ends of these bones as well as the right astragalus and calcaneum exhibit some features that appear to be abnormalities rather than artifacts of postmortem compression or crushing. The tibia is slightly shorter than the femur. The tibiofemoral ratio is 0.89 , which lies within the range recorded for Herrerasaurus ( $0.87-0.91$ ) (Novas 1994). The proximal end of the tibia is subtriangular with its long axis directed anteroposteriorly. The cnemial crest projects anteriorly and extends along the proximal one fifth of the tibia. The lateral condyle is posteriorly located as in Herrerasaurus. In cross-section, the proximal half of the shaft is elliptical and the distal half subcircular. In lateral view, the anterior margin of the tibial shaft ventral to the cnemial crest is straight, whereas it is concave in Herrerasaurus (Novas 1994: Fig. 8B). In distal view the distal end of the tibia is subcircular, rather than quadrangular, more closely resembling the condition in Staurikosaurus (Galton 1977) than in Herrerasaurus. The posteroventral process is transversally narrower and dorsoventrally shorter than in Herrerasaurus. The distal end of the right tibia, which as mentioned above appears to be pathologic, has an unusual, tab-shaped lateral expansion of the posteroventral process (Figure 7P).

The relatively slender fibula is subequal to the tibia in length and has transversally flattened proximal and distal ends, the former twice the anteroposterior width at the mid shaft. The shaft is slightly bowed anterolaterally, and has a subtriangular crosssection at mid shaft. Poor surface preservation and breakage of the distal end obscure further details.

The astragalus and calcaneum of Sanjuansaurus are fused as in some dinosauromophs (Dromomeron romeri; Irmis et al. 2007), Lagerpeton chanarensis (Romer


Figure 8. Right astragalus and calcaneum of Sanjuansaurus gordilloi (PVSJ 605). Right astragalus and calcaneum in proximal $(\mathbf{A})$, distal $(\mathbf{B})$, anterior $(\mathbf{C})$, posterior $(\mathbf{D})$, lateral $(\mathbf{E})$, and medial views $(\mathbf{F})$. $A b$ breviations: $\boldsymbol{A}$, astragalus; $\boldsymbol{a p}$, ascending process; $\mathbf{C}$, calcaneum; $\boldsymbol{f}$, foramen; $\boldsymbol{p m b}$, posteromedial border; $\boldsymbol{p s}$, posterior shelf; $\boldsymbol{r}$, ridge. Scale bar equals 2 cm .
1971), heterodontosaurids (Santa Luca 1980), and coelophysoid theropods (Raath 1969). Unlike in many coelophysoids, however, there is no fusion between the crus and proximal tarsals. Whereas the complete fusion of proximal tarsals in Sanjuansaurus might be natural, the distal end of the tibia just above the preserved proximal tarsals appears to be pathologic. Thus we are uncertain whether the observed fusion of the preserved right proximal tarsals is natural or a pathological condition. The astragalus is subtriangular in dorsal view, with a rounded posteromedial border, instead of the distinct posteromedial corner present in Herrerasaurus (Figure 8A, B). The ascending process is tabular, extending transversally from the medial border of the astragalus mediolaterally along the entire width of the astragalus (Figure 8A, B). In Sanjuansaurus, the tip of the ascending process is located at one fifth the length of the lateral border, as in Herrerasaurus, but is close to the anterior border in the former, whereas in the latter it is close to the posterior border. Lateral to its tip, the ascending process continues as a ridge on the proximomedial surface of the calcaneum (Figure 8A). The anterior surface of the ascending process is pierced by a large foramen near its base, as in Herrerasaurus


Figure 9. Single most parsimonious tree (MPT) resulting from the present parsimony analysis (tree length 190 steps; consistency index 0.553 , retention index 0.593 ).
(Novas 1994). The posterior portion of the astragalus is flat with a sharp posterior edge that forms a posteriorly projecting shelf (Figure 8E, F).

A complete left second metatarsal is the only pedal bone preserved. It is straight in dorsal view (Figure 7O). The proximal end is transversely flattened with the long axis directed anterolaterally as in Herrerasaurus (Novas 1994). A pair of distinct articular surfaces for the first and third metatarsals is present on the medial and lateral sides of the proximal part of the shaft. The proximal articular surface is subrectangular in proximal view. The narrow shaft is twisted so that, in distal view, proximal and distal ends have undergone a clockwise rotation of $45^{\circ}$. The distal end of the metatarsal is asymmetrical, with the lateral condyle extending further distally than the medial condyle. The lateral condyle is more developed than the medial and has a deeper collateral ligament fossa. The distal end has a transversely broad dorsal extensor depression to accommodate the base of the proximal pedal phalanx. The depression is bounded proximally by a ridge, which is more prominent laterally than medially. These features also characterize the second metatarsal of Herrerasaurus (Novas 1994).

## Discussion

Sanjuansaurus gordilloi exhibits several features that allow its distinction from all other known basal dinosaurs:

1. Shelf-like, posterolaterally directed transverse processes in posterior cervical vertebrae. In Sanjuansaurus from the fifth cervical vertebra back, the transverse processes increase in anteroposterior width and transverse length, and project posteroventrolaterally (Figure 5B), an unusual shape among basal dinosaurs. In other basal dinosaurs the transverse process are shorter or triangular (e.g. Herrerasaurus, Staurikosaurus, Eoraptor, Tawa, Adeopapposaurus; Sereno et al. 1993; Sereno and Novas 1994; Bittencourt and Kellner 2009; Martinez 2009; Nesbitt et al. 2009).
2. Neural spines of the sixth to eighth dorsal vertebrae, at least, bearing acute anterior and posterior processes. Sanjuansaurus has distinctive pointed processes extending anteriorly and posteriorly from the apex of the preserved anterior dorsal spines (Figure 5C, D). This feature is unique among known dinosaurs.
3. Coracoid with long posteroventral process. In Sanjuansaurus the hook-shaped posteroventral process of the coracoid is long and pointed (Figure 6B), similar to that in ornithomimids such as Gallimimus (Osmólska and Barsbold 1990: Fig. 4). In other basal dinosaurs the posteroventral process of the coracoid is less developed (e.g,, Herrerasaurus, Guaibasaurus, Eoraptor, Tawa, Saturnalia; Sereno et al. 1993; Sereno and Novas 1994; Bonaparte et al. 2007; Langer et al. 2007; Nesbitt et al. 2009)
4. Everted lateral margins of the glenoid. In Sanjuansaurus the rim of the glenoid protrudes laterally in a conspicuous manner (Figure 6A). In the glenoid portion of the bones the margins represent $50 \%$ of the thickness of the scapula and the $60 \%$ the thickness of the coracoid. In other basal dinosaurs the glenoid portions of the scapula and coracoid are the thicker portions of the respective bones, but they lack the everted lateral margins (e.g, Herrerasaurus, Eoraptor, Panphagia, Tawa, Guaibasaurus, Saturnalia; Sereno et al. 1993;Sereno and Novas 1994; Bonaparte et al. 2007; Martinez and Alcober 2009; Nesbitt et al. 2009)
5. Short pubis ( $63 \%$ of the femoral length). In Sanjuansaurus the pubis is very short ( $63 \%$ of the femoral length), shorter than that present in other basal surischians (e.g, Herrerasaurus (91\%), Staurikosaurus (70\%), Tawa (90\%), Eoraptor (80\%).
6. Pronounced rugose scar on the medial surface of the femur at the level of the fourth trochanter. In Sanjuansaurus the scar presumably for the insertion of M. caudifemoralis longus is very large, pronounced and rugose protuberance (Figure 7G). In other basal dinosaurs this scar is relatively small and smooth (e.g., Herrerasaurus, Eoraptor, Panphagia, Tawa, Guaibasaurus, Saturnalia; Sereno et al. 1993; Sereno and Novas 1994; Bonaparte et al. 1999; Langer 2003; Martinez and Alcober 2009; Nesbitt et al. 2009)

These autapomorphies allow us to distinguish Sanjuansaurus gordilloi from other known basal dinosaurs. Furthermore, although Sanjuansaurus and Herrerasaurus are
similar, the new taxon can be further distinguished from the latter form by three other characters: (1) The scapular blade of Sanjuansaurus is straplike in lateral view (Figure 6A, B), similar in shape than that present in Herrerasaurus, but it is narrower in Sanjuansaurus. The minimum width of the blade (near the base) is $54 \%$ the width of the acromial margin, less than that found in either small (83\%; PVSJ 407) or very large individuals ( $60 \%$; PVSJ 053) of Herrerasaurus. (2) The pubis shaft of Sanjuansaurus lacks the strong proximal curvature characteristic of Herrerasaurus (Novas 1994). (3) In Sanjuansaurus the obturator foramen of the pubis is larger. The anteroposterior diameter of the obturator foramen of Sanjuansaurus measures 34\% of the anteroposterior width of the proximal end of the pubis, whereas that value is 15\% in Herrerasaurus.

## Phylogenetic Position

Phylogenetic analysis resulted in a single most parsimonious tree of 190 steps (consistency index 0.553 , retention index 0.593 ). An implicit enumeration search (Goloboff et al. 2003) and jackknifing (probability of character removal $0.36,1,000$ resampled matrices) were also performed. The topology of the most parsimonious tree is similar to the consensus tree recovered by Martinez and Alcober (2009), differing mainly in resolved positions for Silesaurus and Guaibasaurus. In the present analysis Silesaurus was positioned outside Dinosauria, and Guaibasaurus was positioned as a non-eusaurischian saurischian as in the analysis by Langer and Benton (2006).

The analysis supports the hypotheses that Dinosauria and Herrerasauridae (Staurikosaurus pricei + Herrerasaurus ischigualastensis + Sanjuansaurus gordilloi) are monophyletic and that Herrerasauridae is positioned at the base of Saurischia outside of Eusaurischia, a result similar to that presented by Langer and Benton (Langer and Benton 2006). Within Herrerasauridae, a polytomy was obtained between Staurikosaurus, Sanjuansaurus and Herrerasaurus.

Seven synapomorphies support the clade Herrerasauridae in the consensus tree (characters 20.1, 39.1, 45.1, 46.1, 47.1, 69.2, and 77.1). Only four of those (characters $39,45,46$, and 77) can be scored in all herrerasaurids, and character 20 is the only one that cannot be determined in Sanjuansaurus. The unambiguous synapomorphies that unite the herrerasaurids in this analysis are the same as those previously identified (Langer and Benton 2006), and do not modify our understanding of the monophyly of Herrerasauridae, although they clearly recover Sanjuansaurus as herrerasaurid.

Other features that support a grouping Sanjuansaurus + Herrerasaurus, but are ambiguous at present include: a narrow "U" shaped antorbital fossa with a promaxillary fenestra located on the anterodorsal border; centrum of the sixth cervical vertebra longest in the cervical series; spine tables on the distal end of the last dorsal and the sacral neural spines; two sacral vertebrae with the addition of one incipient dorsosacral; strap-shaped scapular blade that forms an angle of more than $90^{\circ}$ with the
acromion; size and shape of the pubic foot; and sinuous lateral border of the pubis in anterior view. There are a few ambiguous character-states shared by Sanjuansaurus and Staurikosaurus but not with Herrerasaurus: shortness of the pubis relative to the femur and the subcircular distal end of the tibia in distal view. The latter character was originally considered as an autapomorphy of Staurikosaurus (Bittencourt and Kellner 2009).

On the other hand, many characters of Sanjuansaurus are unlike those inother herrerasaurids (where known): long band-shaped transverse processes of the distal cervicals; deep lateral and ventral concavity in cervical and dorsal centra; short pubis with wide subcircular obturator foramen; and fused astragalus and calcaneum with a tabular ascending process (if this character-state is not pathological in origin).

## Faunal Considerations

The co-occurrence in the basal portion of the Ischigualasto Formation, of two herrerasaurids (Sanjuansaurus, Herrerasaurus), a basal saurischian (Eoraptor), and two sauropodomorphs (Panphagia, Chromogisaurus) suggests that saurischian dinosaurs were already highly diversified in southwestern Pangea early in the Late Triassic. The new herrerasaurid also represents another large-bodied predatory dinosaur in the Carnianage Ischigualasto fauna, contrasting with the rarity of carnivorous dinosaurs in the successive Norian assemblage of the overlaying Los Colorados Formation. In that richly represented assemblage, only a single specimen of a coelophysoid theropod has been recovered to date (Arcucci and Coria 2003). Carnivorous crurotarsan archosaurs dominate this Norian fauna, underscoring a complex pattern of faunal change. The faunal assemblages of Ischigualasto Basin strengthen the theory of a complex early radiation of dinosaurs (Brusatte et al. 2010), controlled by a succession of events developed during the Late Triassic, in opposition to models of gradual dominance by competition (Bonaparte 1982; Charig 1984), rapid diversification in the late Carnian (Padian and May 1993); opportunistic radiation in the Norian and Early Jurassic (Benton 1993; Benton 2006), dinosaurian dominance in the Norian (Novas 1996), or early diversification in the Carnian and increase in diversity and abundance in the Norian (Langer et al. 2010).

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## References

Arcucci AB, Coria RA (2003) A new Triassic carnivorous dinosaur from Argentina. Ameghiniana 40: 217-228.
Benedetto JL (1973) Nueva familia de saurisquios triásicos. Ameghiniana 10: 89-102.
Benton MJ (1990) Origin and interrelationships of dinosaurs. In: Weishampel DB, Dodson P, Osmólska H (Eds) The Dinosauria. University of California Press, Berkeley, 11-30.
Benton MJ (1993) Late Triassic extinctions and the origin of dinosaurs. Science 260: 769-770.
Benton MJ (2006) The origin of the dinosaurs. III Jornadas Internacionales sobre Paleontología de Dinosaurios y su Entorno, Actas 1: 11-19.
Bittencourt SB, Kellner AWA (2009) The anatomy and phylogenetic position of the Triassic dinosaur Staurikosaurus pricei Colbert, 1970. Zootaxa 2079: 1-56.
Bonaparte JF (1982) Faunal replacement in the Triassic of South America. Journal of Vertebrate Paleontology 2: 362-371.
Bonaparte JF, Pumares JA (1995) Notas sobre el primer cráneo de Riojasaurus incertus (Dinosauria, Prosaurópoda, Melanorosauridae) del Triásico superior de La Rioja. Ameghiniana 32: 341-349.
Bonaparte JF, Brea G, Schultz CL, Martinelli AG (2007) A new specimen of Guaibasaurus candelariensis (basal Saurischia) from the Late Triassic Caturrita Formation of southern Brazil. Historical Biology 19: 73-82.
Brinkman DB, Sues H-D (1987) A staurikosaurid dinosaur from the Upper Triassic Ischigualasto Formation of Argentina and the relationships of the Staurikosauridae. Palaeontology 30: 493-503.
Brusatte SL, Nesbitt SJ, Irmis RB, Butler RJ, Benton MJ, Norell MA (2010) The origin and early radiation of dinosaurs. Earth-Science Reviews 101: 68-100.
Charig AJ (1984) Competition between tharepsids and archosaurs during the Triassic period: a review and syntesis of current theories. Zoological Society of London Symposium 57: 597-628.
Colbert EH (1970) A saurischian dinosaur from the Triassic of Brazil. American Museum Novitates 2405: 1-39.
Currie BS, Colombi CE, Tabor NJ, Shipman TC, Montañez IP (2009) Stratigraphy and architecture of the Upper Triassic Ischigualasto Formation, Ischigualasto Provincial Park, San Juan, Argentina. Journal of South American Earth Sciences 27: 74-87.
Ezcurra MD (2006) A review of the systematic position of the dinosauriform archosaur Eucoelophysis baldwini Sullivan \& Lucas, 1999 from the Upper Triassic of New Mexico, USA. Geodiversitas 28: 649-684.
Ezcurra MD (2008) A new early dinosaur from the Carnian Ischigualasto Formation (NW Argentina) and the origin of dinosaurs. Libro de Resúmenes, III Congreso Latinoamericano de Paleontología de Vertebrados, Neuquén, Patagonia, Argentina, 87.
Ezcurra MD (2010) A new early dinosaur (Saurischia: Sauropodomorpha) from the Late Triassic of Argentina: a reassessment of dinosaur origin and phylogeny. Journal of Systematic Palaeontology 8: 371-425.

Ezcurra MD, Cuny G (2007) The coelophysoid Lophostropheus airelensis, gen. nov.: a review of the systematics of "Liliensternus" airelensis from the Triassic-Jurassic outcrops of Normandy (France). Journal of Vertebrate Paleontology 27: 73-86.
Ezcurra MD, Novas FE (2007) Phylogenetic relationships of the Triassic theropod Zupaysaurus rougieri from NW Argentina. Historical Biology 19: 35-72.
Fraser NC, Padian K, Walkden KD, Davis LM (2002) Basal dinosauriform remains from Britain and the diagnosis of the Dinosauria. Palaeontology 45: 79-95.
Galton PM (1977) On Staurikosaurus pricei, an early saurischian dinosaur from the Triassic of Brazil, with notes on the Herrerasauridae and Poposauridae. Paläontologische Zeitschrift 51: 234-245.
Galton PM (2000) Are Spondylosoma and Staurikosaurus (Santa Maria Formation, MiddleUpper Triassic, Brazil) the oldest saurischian dinosaurs? Paläontologische Zeitschrift 74: 393-423.
Gauthier J (1986) Saurischian monophyly and the origin of birds. In: Padian K (Ed) The origin of birds and the evolution of flight. Memoirs of the California Academy of Sciences 8, 1-55.
Goloboff PA, Farris JS, Nixon K (2003) TNT: tree analysis using new technologies. Program and documentation available from the authors and at http://www.zmuc.dk/public/phylogeny.
Holtz TR (1995) A new phylogeny of Theropoda. Journal of Vertebrate Paleontology 15 (Supplement to 3): 35A.
Irmis RB, Nesbitt SJ, Padian K, Smith ND, Turner AH, Woody D, Downs A (2007) A Late Triassic dinosauromorph assemblage from New Mexico and the rise of dinosaurs. Science 317: 358-361.
Kellner AWA, Campos DA (2000) Brief review of dinosaur studies and perspectives in Brazil. Anais da Academia Brasileira de Ciências 72: 509-538.
Langer MC (2003) The pelvic and hind limb anatomy of the stem-sauropodomorph Saturnalia tupiniquim (Late Triassic, Brazil). PaleoBios 23: 1-30.
Langer MC (2004) Basal Saurischians. In: Weishampel DB, Dodson P, Osmólska H (Eds) The Dinosauria, Second edition. University of California Press, Berkeley, 25-46.
Langer MC, Benton MJ (2006) Early dinosaurs: a phylogenetic study. Journal of Systematic Palaeontology 4: 309-358.
Langer MC, Franca MAG, Gabriel S (2007) The pectoral girdle and forelimb anatomy of the stem-sauropodomorph Saturnalia tupiniquim (Late Triassic, Brazil). In: Barrett PM, Batten DJ (Eds) Evolution and palaeobiology of early sauropodomorph dinosaurs. Special Papers in Palaeontology 77: 113-137.
Langer MC, Abdala F, Richter M, Benton MJ (1999) A sauropodomorph dinosaur from the Upper Triassic (Carnian) of southern Brazil. Comptes Rendus de l'Academie des Sciences, Paris 329: 511-517.
Langer MC, Ezcurra MD, Bittencourt JS, Novas FE (2010) The origin and early evolution of dinosaurs. Biological Reviews of the Cambridge Philosophical Society 84: 55-110.
Long RA, Murry PA (1995) Late Triassic (Carnian and Norian) tetrapods from the Southwestern United States. New Mexico Museum of Natural History \& Science Bulletin 4: 1-254.

Martinez RN (2009) Adeopapposaurus mognai, gen. et sp. nov. (Dinosauria: Sauropodomorpha), with comments on adaptations of basal Sauropodomorpha. Journal of Vertebrate Paleontology 29: 142-164.
Martinez RN, Alcober OA (2009) A basal sauropodomorph (Dinosauria: Saurischia) from the Ischigualasto Formation (Triassic, Carnian) and the Early Evolution of Sauropodomorpha. PLoS ONE 4: 1-12.
Martínez RN, Sereno PC, Alcober OA (2008) A new basal theropod from the Ischigualasto Formation of San Juan Province, Argentina. Libro de Resúmenes, III Congreso Latinoamericano de Paleontología de Vertebrados, Neuquén, Patagonia, Argentina, 153.
Nesbitt SJ, Irmis RB, Parker WG (2007) A critical reevaluation of the Late Triassic dinosaur taxa of North America. Journal of Systematic Palaeontology 5: 209-243.
Nesbitt SJ, Smith ND, Irmis RB,Turner AH, Downs A, Norell MA (2009) A Complete skeleton of a Late Triassic saurischian and the early evolution of dinosaurs. Science 326: 15301533.

Novas FE (1986) Un probable teropodo (Saurischia) de la Formación Ischigualasto (Triásico Superior), San Juan, Argentina. IV Congreso Argentino de Paleontología y Bioestratigrafía, Mendoza 2: 1-6.
Novas FE (1992) Phylogenetic relationships of the basal dinosaurs, the Herrerasauridae. Palaeontology 35: 51-62.
Novas FE (1994) New information on the systematics and postcranial skeleton of Herrerasaurus ischigualastensis (Theropoda: Herrerasauridae). Journal of Vertebrate Palaeontology 13: 400-423.
Novas FE (1996) Dinosaur monophyly. Journal of Vertebrate Paleontology 16: 723-741.
Novas FE (1997) Herrerasauridae. In: Currie PJ, Padian K (Eds) Encyclopedia of Dinosaurs. Academic Press, San Diego, 303-311.
Osmólska H, Barsbold R (1990) Troodontidae. In: Weishampel DB, Dodson P, Olmólska H (Eds) The Dinosauria. University of California Press, Berkeley, 259-268.
Padian K, May C (1993) The earliest dinosaurs. In: Lucas SG, Morales M (Eds) The nonmarine Triassic. New Mexico Museum Natural History \& Science Bulletin 3: 379-381.
Raath M (1969) A new coelurosaurian dinosaur from the Forest Sandstone of Rhodesia. Arnoldia 4: 1-25.
Rauhut OWM (2003) The interrelationships and evolution of basal theropod dinosaurs. Special Papers in Palaeontology 69: 1-213.
Reig OA (1963) La presencia de dinosaurios saurisquios en los "Estratos de Ischigualasto" (Mesotriásico superior) de las provincias de la San Juan y La Rioja (Republica Argentina). Ameghiniana 3: 3-20.
Renne PR, Mundil R, Balco G, Min K, Ludwig KR (2010) Joint determination of 40K decay constants and $40 \mathrm{Ar}^{*} / 40 \mathrm{~K}$ for the Fish Canyon sanidine standard, and improved accuracy for 40Ar/39Ar geochronology. Geochimica et Cosmochimica Acta 74: 5349-5367.
Romer AS (1971) The Chañares (Argentina) Triassic reptile fauna X. Two new but incompletely known long-limbed pseudosuchians. Breviora 378: 1-10.
Santa Luca AP (1980) The postcranial skeleton of Heterodontosaurus tucki (Reptilia, Ornithischia) from the Stormberg of South Africa. Annals of South African Museum 79: 159-211.

Rogers RR, Swisher III CC, Sereno PC, Monetta AM, Forster CA (1993) The Ischigualasto tetrapod assemblage, Late Triassic, Argentina, and $40 \mathrm{Ar} / 39 \mathrm{Ar}$ dating of dinosaurs origins. Science 260: 794-797.
Sereno PC (1994) Pectoral girdle and forelimb of the basal theropod Herrerasaurus ischigualastensis. Journal of Vertebrate Paleontology 13: 425-450.
Sereno PC (1999) The evolution of dinosaurs. Science 284: 2137-2147.
Sereno PC (2005) TaxonSearch: Database for Suprageneric Taxa \& Phylogenetic Definitions. http://www.taxonsearch.org/
Sereno PC (2007) The phylogenetic relationships of early dinosaurs: a comparative report. Historical Biology 19: 145-155.
Sereno PC, Novas FE (1992) The complete skull and skeleton of an early dinosaur. Science 258: 1137-1140.
Sereno PC, Novas FE (1994) The skull and neck of the basal theropod Herrerasaurus ischigualastensis. Journal of Vertebrate Paleontology 13: 451-476.
Sereno PC, Forster CA, Rogers RR, Monetta AM (1993) Primitive dinosaur skeleton from Argentina and the early evolution of the Dinosauria. Nature 361: 64-66.
Smith ND, Makovicky PJ, Hammer WR, Currie PJ (2007) Osteology of Cryolophosaurus ellioti (Dinosauria: Theropoda) from the Early Jurassic of Antarctica and implications for early theropod evolution. Zoological Journal of the Linnean Society 151: 377-421.
Welles SP (1984) Dilophosaurus wetherilli (Dinosauria, Theropoda): osteology and comparisons. Palaeontographica A 185: 85-180.
Wilson JA (1999) A nomenclature for vertebral laminae in sauropods and other saurischian dinosaurs. Journal of Vertebrate Paleontology 19: 639-653.
Wilson JA (2006) Anatomical nomenclature of fossil vertebrates: standardized terms or 'lingua franca'?. Journal of Vertebrate Paleontology 26: 511-518.
Witmer LM (1997) The evolution of the antorbital cavity of archosaurs: a study in soft tissue reconstruction in the fossil record with an analysis of the function of pneumaticity. Society of Vertebrate Paleontology Memoir 3: 1-73.

