

Unravelling the goblin spiders puzzle: rDNA phylogeny of the family Oonopidae (Araneae)

CHARLOTTE DE BUSSCHERE^{*,1}, WOUTER FANNES², ARNAUD HENRARD^{2,3},
EVA GAUBLOMME¹, RUDY JOCQUÉ² & LÉON BAERT¹

¹O.D. Taxonomy and Phylogeny, Royal Belgian Institute of Natural Sciences, Brussels, Belgium; Charlotte de Busschere* [Charlotte.debusschere@gmail.com], Eva Gaublomme [Egaublomme@yahoo.com], Léon Baert [Leon.baert@naturalsciences.be] — ²Section Invertebrates non-insects, Royal Museum for Central Africa, Tervuren, Belgium; Wouter Fannes [Wouter.fannes@africamuseum.be], Arnaud Henrard [Arnaud.henrard@gmail.com], Rudy Jocqué [Rudy.jocque@africamuseum.be] — ³Earth and Life Institute, Biodiversity research Center, Université Catholique de Louvain, Louvain la Neuve, Belgium — * Corresponding author

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Abstract

The mega-diverse haplogyne family of goblin spiders (Oonopidae Simon, 1890) has long been among the most poorly known families of spiders. However, since the launch of the goblin spider Planetary Biodiversity Inventory project knowledge about Oonopidae is rapidly expanding. Currently, Oonopidae is placed within the superfamily Dysderoidea and is divided into three subfamilies. Nevertheless, the monophyly and internal phylogeny of this family has not yet been investigated based on DNA sequence data. Hence, this study reports the first phylogeny based on ribosomal sequence data including 37 oonopid genera and representatives of all families within the Dysderoidea. These results suggest that the majority of the oonopid genera constitute a natural group. Moreover, two subfamilies Orchestinae and Sulsulinae and several morphologically defined groups e.g. the *Zyngoonops*- and *Dysderina*-groups, were well supported. In contrast, the *Pelcinus*-, *Stenoonops*- and *Scaphiella*-groups were not corroborated. Although most genera represented by more than one specimen were recovered as monophyletic, our study casts doubt on the monophyly of the genus *Aschnaonops* Makhan & Ezzatpanah, 2011. Furthermore, the results corroborate that a low degree of body sclerotisation might be considered as a plesiomorphic trait.

Key words

18S, 28S, Orsolobidae, Dysderoidea, Trogloraptoridae.

1. Introduction

Goblin spiders (Oonopidae) are small haplogyne spiders, ranging in size from 0.8 to 3 mm. They occur throughout the temperate and tropical regions of the world in a large range of habitats such as deserts, mangroves, savannahs and rainforests (JOCQUÉ & DIPPENAAR-SCHOEMAN 2006; FANNES et al. 2008; GRISMADO 2010). On a smaller scale, goblin spiders can be found in litter (UBICK 2005), canopy (FANNES et al. 2008) or even in caves (HARVEY & EDWARD 2007). Oonopidae are also well represented in the fossil record; more precisely, several oonopid fos-

sil species have been found in various ambers (PENNEY 2006; DUNLOP et al. 2012). Most fossil species have been assigned to the genus *Orchestina* Simon, 1882, indicating that this genus was already widespread by the end of the Cretaceous (SAUPE et al. 2012). Currently goblin spiders include more than 1325 recognized species and 97 genera (PLATNICK 2013), but this might be regarded as a fraction of the total diversity as it is estimated that between 2000 and 2500 species might exist worldwide (PLATNICK 2006; AGNARSSON et al. 2013). This underestimation of oonopid

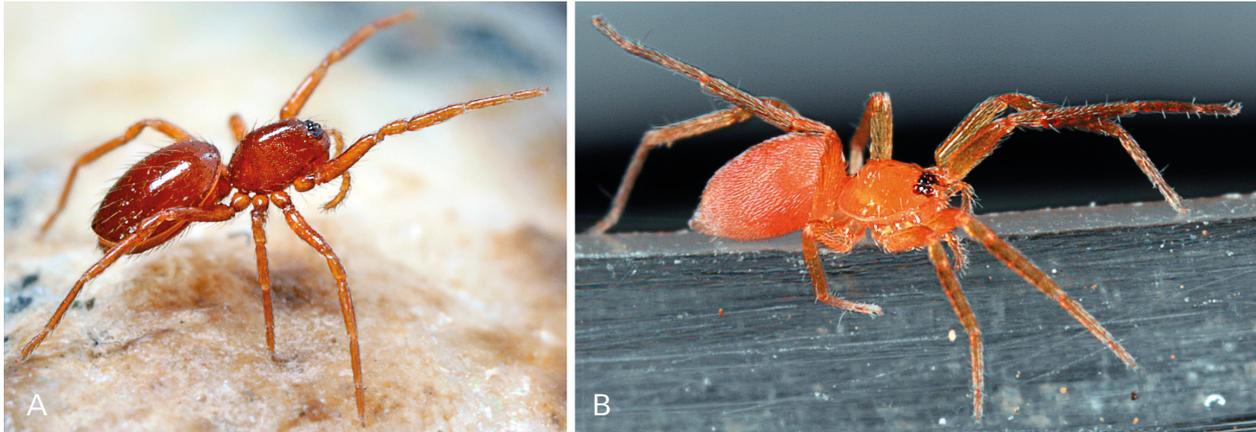


Fig. 1. The spider family Oonopidae is characterized by a high level of morphological diversity in traits such as the degree of body sclerotisation, ranging from heavily sclerotized taxa within the Oonopinae, e.g. *Silhouettella loricatea* (A), to soft-bodied oonopids, e.g. *Oonops placidus* (B). (Pictures from A. Henrard)

diversity could be related to their small size, their wide geographic distribution, their occurrence in different microhabitats and the rather recent use of adequate sampling techniques such as knock-down fogging (PLATNICK 2006). The U.S. National Science Foundation (NSF) funded the goblin spider Planetary Biodiversity Project (PBI) from 2006 in which more than 45 researchers were involved with the aim to revise this mega-diverse family. Since the start of this goblin spider PBI project, a tremendous amount of taxonomic work has been done with the result of a twofold increase in described species and more than 70 publications. Based upon these thorough revisions of several genera, a high level of morphological diversity is observed within this family in traits such as carapace shape and ornamentation, arrangement and number of eyes, genital morphology and degree of body sclerotisation ranging from soft-bodied taxa e.g. *Oonops* Templeton, 1835 to heavily sclerotized taxa e.g. *Silhouettella* Benoit, 1979 (Fig. 1). Additionally, sexual dimorphism is observed in several genera e.g. *Unicorn* Platnick & Brescovit, 1995 and *Brignolia* Dumitrescu & Georgescu, 1983.

However, our current knowledge of the phylogeny of the Oonopidae is severely limited and solely based upon morphological data. Hitherto, Oonopidae is placed as the sister group of the family Orsolobidae within the superfamily Dysderoidea based upon the morphological analyses of PLATNICK et al. (1991) and RAMÍREZ (2000). The remnant families within the Dysderoidea are the Segestriidae and Dysderidae. GRISWOLD et al. (2012) suggested that the recently described family Trogloraptoridae might be a primitive member of the Dysderoidea based on spinneret morphology among others. Orsolobidae and Oonopidae are suggested to be sister groups based upon (1) the presence of only two tarsal claws, (2) claw dentition bipectinate (although few oonopids have unipectinate claws, such as *Oonops pulcher* Templeton, 1835, *Tapinesthis inermis* Simon, 1882 or *Birabenella* Grismado, 2010; PLATNICK & DUPÉRRÉ 2009c; HENRARD & JOCQUÉ 2012) and (3) the presence of propriocep-

tor bristles on the tarsi (FORSTER & PLATNICK 1985; PLATNICK et al. 1991; RAMÍREZ 2000). The monophyly of the Oonopidae is based upon the presence of a completely fused, unpaired testis; female palp lacking a claw; tarsal organ flat, exposed or capsulate, with a distinctive longitudinal ridge originating at the proximal end of the organ; legs I and II with one more tarsal organ receptor than legs III and IV (BURGER 2009; BURGER & MICHALIK 2010; PLATNICK et al. 2012).

However, monophyly of this family has not yet been adequately tested with molecular data. Additionally, the internal phylogeny of the Oonopidae is rather poorly investigated. Hitherto, cladistic analyses have been limited to species-level work (HENRARD & JOCQUÉ 2012; ANDRIAMALALA & HORMIGA 2013; FANNES 2013) solely based on morphological data. At the supraspecific level, PLATNICK et al. (2012) recognized three subfamilies within the Oonopidae: the Orchestininae (containing only the soft-bodied genus *Orchestina*), the Sulsulinae (containing the soft-bodied genera *Sulsula* Simon, 1882, *Dalmasula* Platnick, Szűts & Ubick, 2012, *Unicorn*, *Xiombarg* Brignoli, 1979, *Puan* Izquierdo, 2012 and *Cortestina* Knoflach, 2009) and the Oonopinae (containing all the remaining genera, including those with a heavily sclerotized abdomen). The Orchestininae and Sulsulinae are treated as more primitive oonopid subfamilies (PLATNICK et al. 2012) based upon the presence of a well-sclerotized sperm duct in the bulbus, a feature also found in Orsolobidae and all other spiders (FORSTER & PLATNICK 1985; PLATNICK et al. 2012). PLATNICK et al. (2012) consider the soft-bodied New Zealand genus *Kapitia* Forster, 1956 as the sister group of other Oonopinae. Furthermore, within the higher Oonopinae, a distinction can be made between soft-bodied genera such as *Birabenella*, *Oonops*, *Neotrops* Grismado & Ramírez, 2014 and *Oonopinus* Simon, 1893 and hard-bodied (armoured) genera (Fig. 1). These are characterized by a distinctly sclerotized abdomen, and have been considered to constitute a monophyletic group (PLATNICK & DUPÉRRÉ 2010b; PLATNICK et al. 2012). Within the armoured oonopids, six large ge-

nus groups have so far been recognized based on putative synapomorphies: the *Stenoonops*-group (PLATNICK & DUPÉRRÉ 2010b), the *Dysderina*-group (PLATNICK & DUPÉRRÉ 2011b,a, 2012), the *Scaphiella*-group (PLATNICK & DUPÉRRÉ 2009a, 2010c, 2011c), the *Pelcinus*-group (ÁLVAREZ-PADILLA et al. 2012; PLATNICK et al. 2012), the Gamasomorphoids (ÁLVAREZ-PADILLA et al. 2012) and the *Zyngoonops*-group (FANNES 2012). However, as noted above, these subfamilies and genus groups are not based on quantitative phylogenetic analyses, and their validity thus remains to be tested.

The main goals of this study are to infer the first phylogeny of the Oonopidae based on ribosomal DNA sequence data and to use this phylogeny to evaluate how well several morphologically defined groups delineate well supported phylogenetic relationships.

2. Materials and methods

2.1. Taxon sampling

The dataset includes 106 Oonopidae taxa representing 36 genera and stemming from different continents and several specimens representing Segestriidae, Orsolobidae, Dysderidae and Trogloraptoridae (Table 1). A few specimens representing the Filistatidae and Liphistiidae were included as outgroup taxa. Specimens or tissue of specimens were provided by members of the PBI project. Specimens were collected from 2001 until 2012 by different sampling techniques (mainly sieving, pitfall trapping, fogging, hand collecting). Fixation and preservation conditions of the collected specimens might have varied among collectors. Most specimens were sampled and stored in 70% ethanol which is common for morphological work. A minority of the samples was fixed and stored directly in 97% ethanol at -20°C . Specimens were identified to family, genus and/or species level by members of the PBI project (Table 1).

2.2. DNA extraction, amplification and sequencing

Samples were extracted with a NucleoSpin® tissue kit (Macherey-Nagel, Düren) according to the manufacturer's protocol. Three overlapping fragments of *18S* (c. 1800 nt) were amplified using the following primer pairs: 18S1F/18S5R (c. 820 nt), 18S3F/18SBI (c. 850 nt) and 18Sa2.0/18S9R (c. 650 nt) (GIRIBET et al. 1996). In addition, partial fragments of the *28S* ribosomal DNA were sequenced with the primer pair: 28SZX1/28SC (c. 1200 nt)

(MALLATT & SULLIVAN 1998; HEDIN & MADDISON 2001). Polymerase chain reaction was initiated with an initial denaturation at 95°C for 2'30" followed by 35 (*18S*, *28S*) cycles. Each cycle started with a denaturation at 95°C (30") followed by an annealing step of 30" (annealing temperatures 18S1F/18S5R: 57°C ; 18S3F/18SBI: 58°C ; 18Sa2.0/18S9R: 48°C ; 28SZX1/28SC: 48.5°C). Each cycle ended with an extension step at 72°C (1'30"). Genbank accession numbers are provided in Table 1. DNA samples are deposited in the Royal Belgian Institute of Natural Sciences (Belgium, Brussels) and stored at -20°C . Sequence data for missing outgroup specimens were obtained from NCBI Genbank (Table 1). Approximately 97% of the sequences are new from this study (Table 1).

2.3. Alignment procedures

Sequences were edited and assembled in SeqScape Software v2.5 (Applied Biosystems, Foster City, CA, USA). *18S* sequences were aligned based on two methods resulting in (1) a MAFFT alignment, based on the E-INS-I algorithm of the program package MAFFT (KATO et al. 2002) implemented online (MAFFT version 7 (KATO & STANDLEY 2013), default settings), and (2) a structure informed manual alignment taking into account the established secondary structure of *Androctonus australis* Ewing, 1928 (Accession number: X77908 available at: <http://www.rna.cbb.utexas.edu>). Based upon the information of the secondary structure of *A. australis*, unpaired (loop) and paired (stem) regions were delimited. *28S* sequences were aligned solely based on the E-INS-I algorithm (MAFFT) as only a partial fragment of the *28S* was obtained. Poorly aligned positions were eliminated from the *28S* alignment by using the most relaxed options in Gblocks 0.91b (CASTRESANA 2000; DEREPPER et al. 2008). A concatenated *18S*-*28S* alignment was created by concatenating the MAFFT *18S* and *28S* alignments. Estimates of average evolutionary divergence within each species, genus and family were obtained by calculating the number of base differences per site within each group in MEGA5 (TAMURA et al. 2011).

2.4. Phylogenetic analyses

Phylogeny reconstructions were obtained using Maximum Parsimony (MP), Maximum Likelihood (ML) and Bayesian Inference (BI). Gaps were treated as missing data. MP analyses were conducted with PAUP*4.0b10 (SWOFFORD 1993, 2002). MP analyses were initiated with 1000 random addition sequence replicates with TBR branch swapping and a time limit of 20 s per replicate in PAUP*. The most parsimonious trees were filtered from

Table 1. Summary of specimen information. Column “Genus”: undescribed genera have been assigned five-letter codes according to the PBI-conventions. Columns “18S” and “28S”: Genbank accession numbers in italics are not from this study.

Family	Subfamily	GENUS	SPECIES	SEX	DNA-nr	PBI-nr	COUNTRY	CONTINENT	YEAR	COLL. / DET.	18S	28S
Oonopidae	Oonopinae	<i>Dysderina</i>	<i>tiputini</i>	M	220	15091	Ecuador	South America	2009	M. Ramirez	KF929114	KF929158
Oonopidae	Oonopinae	<i>Paradyserina</i>	<i>fusiscuta</i>	F	265	597	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929115	KF929159
Oonopidae	Oonopinae	<i>Paradyserina</i>	<i>righty</i>	F	272	587	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929116	KF929160
Oonopidae	Oonopinae	<i>Paradyserina</i>	<i>wlad</i>	M	221	15092	Ecuador	South America	2009	M. Ramirez	KF929118	—
Oonopidae	Oonopinae	<i>Paradyserina</i>	<i>wlad</i>	M	224	15103	Ecuador	South America	2009	M. Ramirez	KF929119	KF929162
Oonopidae	Oonopinae	<i>Paradyserina</i>	<i>yanayacu</i>	M	204	30842	Ecuador	South America	2009	M. Ramirez	KF929117	KF929161
Oonopidae	Oonopinae	<i>Scaphiysderina</i>	<i>cotopaxi</i>	M	269	574	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929120	KF929164
Oonopidae	Oonopinae	<i>Scaphiysderina</i>	<i>tandapi</i>	F	278	554	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929121	KF929163
Oonopidae	Oonopinae	<i>Aschnaonops</i>	<i>cosanga</i>	F	202	30839	Ecuador	South America	2009	M. Ramirez	KF929106	KF929151
Oonopidae	Oonopinae	<i>Aschnaonops</i>	<i>silvae</i>	M	212	30831	Ecuador	South America	2009	M. Ramirez	KF929108	—
Oonopidae	Oonopinae	<i>Aschnaonops</i>	<i>tiputini</i>	M	211	30830	Ecuador	South America	2009	M. Ramirez	KF929110	KF929153
Oonopidae	Oonopinae	<i>Bidyserina</i>	<i>perdido</i>	M	203	30840	Ecuador	South America	2009	M. Ramirez	KF929107	KF929152
Oonopidae	Oonopinae	<i>Timadyserina</i>	<i>otonga</i>	F	271	49559	Ecuador	South America	2009	B. Baehr / N. Platnick	KF929109	KF929154
Oonopidae	Oonopinae	<i>Tridyserina</i>	<i>bellavista</i>	F	267	49544	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929111	KF929155
Oonopidae	Oonopinae	<i>Tridyserina</i>	<i>galeras</i>	M	266	49536	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929112	KF929157
Oonopidae	Oonopinae	<i>Tridyserina</i>	<i>jatun</i>	F	209	30834	Ecuador	South America	2009	M. Ramirez	—	KF929156
Oonopidae	Oonopinae	<i>Tridyserina</i>	<i>yasuni</i>	M	226	15105	Ecuador	South America	2009	M. Ramirez	KF929113	—
Oonopidae	Oonopinae	<i>Neoxyphinus</i>	<i>termitophilus</i>	F	99	4778	Argentina	South America	2005	M. Ramirez	KF929122	KF929165
Oonopidae	Oonopinae	<i>Pelicanus</i>	sp.	M	65	5981	Australia	Oceania	—	K. Edward	KF929130	KF929193
Oonopidae	Oonopinae	<i>Silhouettella</i>	<i>loricatula</i>	F	344	—	France	Europe	2012	A. Heniard	KF929095	KF929175
Oonopidae	Oonopinae	<i>Silhouettella</i>	sp.	—	259	3276	Madagascar	Africa	2001	C. Griswold	KF929082	—
Oonopidae	Oonopinae	<i>Escaphiella</i>	<i>gertschi</i>	—	280	16983	Galapagos	South America	2009	L. Baert	KF929125	—
Oonopidae	Oonopinae	<i>Escaphiella</i>	<i>gertschi</i>	—	282	16987	Galapagos	South America	2009	L. Baert	KF929126	KF929197
Oonopidae	Oonopinae	<i>Escaphiella</i>	<i>ramirezi</i>	M	139	14892	Uruguay	South America	2005	M. Ramirez	KF929123	—
Oonopidae	Oonopinae	<i>Escaphiella</i>	<i>schmidti</i>	M	52	29902	Nicaragua	South America	2007	C. Viquez / N. Platnick	KF929124	KF929198
Oonopidae	Oonopinae	<i>Niarchos</i>	<i>barragani</i>	—	277	404	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929129	—
Oonopidae	Oonopinae	<i>Niarchos</i>	<i>bonaldi</i>	—	274	—	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929091	—
Oonopidae	Oonopinae	<i>Scaphios</i>	<i>orellana</i>	M	218	15089	Ecuador	South America	2009	M. Ramirez	KF929092	—
Oonopidae	Oonopinae	<i>Scaphios</i>	<i>yanayacu</i>	M	268	420	Ecuador	South America	2009	PBI expedition / N. Platnick	KF929093	—
Oonopidae	Oonopinae	<i>Birabenella</i>	<i>elqui</i>	F	228	14993	Chile	South America	2009	M. Ramirez	KF929104	—
Oonopidae	Oonopinae	<i>Birabenella</i>	<i>homonota</i>	M	227	14989	Chile	South America	2009	M. Ramirez	KF929105	—
Oonopidae	Oonopinae	<i>Brignolia</i>	<i>kapit</i>	M	292	36337	Brunei	Asia	2009	C. Griswold / Y. Kranz	KF929056	KF929166
Oonopidae	Oonopinae	<i>Brignolia</i>	<i>kapit</i>	M	293	36338	Brunei	Asia	2009	C. Griswold / Y. Kranz	KF929057	KF929167
Oonopidae	Oonopinae	<i>Brignolia</i>	<i>kapit</i>	M	294	36317	Brunei	Asia	2009	C. Griswold / Y. Kranz	KF929058	KF929168
Oonopidae	Oonopinae	<i>Cavisternum</i>	sp.	M	63	5979	Umbrawarra	Australia	—	K. Edward	KF929071	KF929176
Oonopidae	Oonopinae	WFAA	sp.	—	30	—	Congo	Africa	2006	R. Jocqué / W. Fannes	KF929083	KF929190

Table 1 continued.

Oonopidae	Oonopinae	WFAAI	WFAAI2	F	113	—	Ghana	Africa	2005	R. Jocqué / W. Fannes	KF929085	—
Oonopidae	Oonopinae	WFAAI	WF004	—	74	—	Ghana	Africa	2005	R. Jocqué / W. Fannes	KF929084	—
Oonopidae	Oonopinae	WFAAE	sp.	F	115	—	Congo	Africa	2006	R. Jocqué / W. Fannes	KF929050	—
Oonopidae	Oonopinae	WFAAJ	sp.	F	111	—	Guinea	Africa	2008	R. Jocqué / W. Fannes	KF929052	—
Oonopidae	Oonopinae	WFAAQ	sp.	F	50	—	Congo	Africa	2007	R. Jocqué / W. Fannes	KF929051	—
Oonopidae	Oonopinae	<i>Heteroonops</i>	<i>spinimanus</i>	F	144	31069	San Felasco	North America	2007	X. Wang	KF929100	KF929186
Oonopidae	Oonopinae	<i>Heteroonops</i>	<i>spinimanus</i>	—	297	—	Cuba	South America	2010	N. Platnick	KF929101	KF929187
Oonopidae	Oonopinae	<i>Ischnothyreus</i>	<i>petifer</i>	F	284	16986	Galapagos	South America	2009	L. Baert	KF929088	KF929189
Oonopidae	Oonopinae	<i>Ischnothyreus</i>	sp.	F	89	6728	Laos	Asia	2008	P. Jäger	KF929087	—
Oonopidae	Oonopinae	<i>Ischnothyreus</i>	sp.	F	198	—	Congo	Africa	2007	R. Jocqué	KF929086	KF929181
Oonopidae	Oonopinae	<i>Ischnothyreus</i>	sp.	M	95	4777	Queensland	Australia	2006	C. Griswold / C.J. Griswold	KF929089	—
Oonopidae	Oonopinae	<i>Lucetia</i>	<i>distincta</i>	F	298	—	Cuba	South America	2010	N. Platnick	KF929097	—
Oonopidae	Oonopinae	<i>Lucetia</i>	sp.	F	279	16912	Galapagos	South America	2009	L. Baert	KF929096	KF929174
Oonopidae	Oonopinae	<i>Melchisedec</i>	<i>thevenot</i>	F	71	9211	Cameroon	Africa	2007	R. Jocqué	KF929134	—
Oonopidae	Oonopinae	<i>Melchisedec</i>	sp.	F	353	32879	Guinea	Africa	2012	A. Henrard	KF929133	—
Oonopidae	Oonopinae	<i>Neotrops</i>	<i>poguzuu</i>	M	136	14910	Argentina	South America	2005	M. Ramirez	KF929075	—
Oonopidae	Oonopinae	<i>Neotrops</i>	<i>labarqueti</i>	M	140	14891	Uruguay	South America	2005	M. Ramirez	KF929076	—
Oonopidae	Oonopinae	<i>Neotrops</i>	<i>labarqueti</i>	F	143	14894	Uruguay	South America	2005	M. Ramirez	KF929077	KF929182
Oonopidae	Oonopinae	<i>Neotrops</i>	<i>pombero</i>	F	94	14770	Argentina	South America	2005	M. Ramirez	KF929078	KF929183
Oonopidae	Oonopinae	<i>Neotrops</i>	<i>waarani</i>	F	206	30836	Ecuador	South America	2005	M. Ramirez	KF929079	KF929184
Oonopidae	Oonopinae	<i>Neotrops</i>	<i>waarani</i>	M	213	30832	Ecuador	South America	2005	M. Ramirez	KF929080	KF929185
Oonopidae	Oonopinae	<i>Tapinesthis</i>	<i>inermis</i>	—	309	—	Belgium	Europe	2010	A. Henrard	KF929098	KF929149
Oonopidae	Oonopinae	<i>Tapinesthis</i>	<i>inermis</i>	M	70	—	Belgium	Europe	2008	R. Jocqué	KF929099	KF929150
Oonopidae	Oonopinae	<i>Farqua</i>	sp.	F	114	—	South Africa	Africa	2008	R. Jocqué	KF929081	—
Oonopidae	Oonopinae	<i>Onops</i>	<i>placidus</i>	—	327	—	Spain	Europe	2010	A. Henrard	KF929021	—
Oonopidae	Oonopinae	<i>Onops</i>	<i>pulcher</i>	F	418	16980	France	Europe	2012	A. Henrard	—	KF929142
Oonopidae	Oonopinae	<i>Onops</i>	<i>pulcher</i>	F	69	—	Belgium	Europe	2008	R. Jocqué	KF929022	KF929144
Oonopidae	Oonopinae	<i>Onops</i>	<i>pulcher</i>	M	421	16977	France	Europe	2012	A. Henrard	—	KF929143
Oonopidae	Oonopinae	<i>Onopaea</i>	<i>yukii</i>	M	148	23366	Queensland	Australia	2008	B. Baehr	KF929065	—
Oonopidae	Oonopinae	<i>Onopaea</i>	sp.	—	149	23342	Queensland	Australia	2008	B. Baehr	KF929063	—
Oonopidae	Oonopinae	<i>Onopaea</i>	sp.	M	36	—	South Africa	Africa	2008	R. Jocqué	KF929061	KF929171
Oonopidae	Oonopinae	<i>Onopaea</i>	sp.	F	49	—	Cameroon	Africa	2007	R. Jocqué	KF929059	KF929169
Oonopidae	Oonopinae	<i>Onopaea</i>	sp.	—	33	—	Congo	Africa	2007	R. Jocqué	KF929062	KF929172
Oonopidae	Oonopinae	<i>Onopaea</i>	<i>deserticola</i>	M	285	16985	Galapagos	South America	2009	L. Baert	KF929060	KF929170
Oonopidae	Oonopinae	<i>Onopaea</i>	<i>olivernashi</i>	F	147	23284	Queensland	Australia	2008	B. Baehr	KF929064	—
Oonopidae	Oonopinae	<i>Onopaea</i>	<i>apicalis</i>	—	286	—	Galapagos	South America	2009	L. Baert	KF929066	—
Oonopidae	Oonopinae	<i>Onopaea</i>	sp.	M	100	4779	Argentina	South America	2004	M. Ramirez	—	KF929173
Oonopidae	Oonopinae	<i>Prethopalpus</i>	<i>tropicus</i>	M	146	10364	Queensland	Australia	2004	B. Baehr	KF929067	—

Table 1 continued.

Family	Subfamily	GENUS	SPECIES	SEX	DNA-nr	PBI-nr	COUNTRY	CONTINENT	YEAR	COLL. / DET.	18S	28S
Onopidae	Onopinae	<i>Opopaea</i>	sp.	M	100	4779	Argentina	South America	2004	M. Ramirez	—	KF929173
Onopidae	Onopinae	<i>Prethopalpus</i>	<i>tropicus</i>	M	146	10364	Queensland	Australia	2004	B. Baehr	KF929067	—
Onopidae	Onopinae	<i>Triaeris</i>	sp.	F	142	14886	Argentina	South America	2008	M. Ramirez	KF929046	—
Onopidae	Onopinae	<i>Triaeris</i>	sp.	F	53	—	Germany	Europe	2008	R. Jocqué / W. Fannes	KF929047	KF929180
Onopidae	Onopinae	<i>Triaeris</i>	sp.	F	214	30833	Ecuador	South America	2009	M. Ramirez	KF929048	—
Onopidae	Onopinae	<i>Triaeris</i>	sp.	F	229	14898	Argentina	South America	2009	M. Ramirez	KF929049	KF929179
Onopidae	Onopinae	<i>Scaphiella</i>	sp.	—	276	—	Argentina	South America	2009	PBI expedition / N. Platnick	KF929127	KF929195
Onopidae	Onopinae	<i>Scaphiella</i>	sp.	M	300	—	Ecuador	South America	2010	N. Platnick	KF929128	KF929196
Onopidae	Onopinae	<i>Onopoides</i>	sp.	—	299	—	Cuba	South America	2005	N. Platnick	KF929102	KF929188
Onopidae	Onopinae	<i>Xyphinus</i>	sp.	—	153	15934	Thailand	Asia	2007	P. Schwendinger / Y. Kranz	KF929068	—
Onopidae	Onopinae	<i>Xyphinus</i>	sp.	F	291	36321	Brunei	Asia	2009	Y. Kranz	KF929070	KF929178
Onopidae	Onopinae	<i>Xyphinus</i>	sp.	—	83	6740	Laos	Asia	2008	P. Jäger	KF929069	KF929177
Onopidae	Onopinae	<i>Stenoanops</i>	sp.	F	302	—	Cuba	South America	2010	N. Platnick	KF929103	—
Onopidae	Onopinae	<i>Australoanops</i>	sp.	—	338	—	South Africa	Africa	2008	R. Jocqué	KF929131	—
Onopidae	Onopinae	<i>Australoanops</i>	sp.	—	341	—	South Africa	Africa	2008	R. Jocqué	KF929132	—
Onopidae	Orchestiminae	<i>Orchestina</i>	sp.	F	96	4774	Chile	South America	2005	M. Ramirez	KF929053	KF929145
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>communis</i>	—	119	16774	Congo	Africa	2007	R. Jocqué	KF929040	—
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>communis</i>	—	157	16775	Congo	Africa	2007	R. Jocqué	KF929041	—
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>fractipes</i>	M	191	—	Congo	Africa	2009	A. Henrard & R. Jocqué	KF929038	—
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>saaristoi</i>	F	196	—	Congo	Africa	2009	A. Henrard & R. Jocqué	KF929090	KF929191
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>cornuta</i>	F	183	16798	Cameroon	Africa	2007	R. Jocqué	KF929044	KF929147
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>crypta</i>	M	185	6774	Congo	Africa	2007	R. Jocqué	KF929045	KF929148
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>fannesi</i>	F	156	8914	South Africa	Africa	2008	R. Jocqué	KF929072	—
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>macroboliata</i>	M	186	6775	Congo	Africa	2007	R. Jocqué	KF929039	—
Onopidae	Orchestiminae	<i>Orchestina</i>	<i>pavesiformis</i>	F	232	30955	Argentina	South America	2010	M. Ramirez	KF929094	—
Onopidae	Orchestiminae	<i>Orchestina</i>	SaWa5	J	237	30913	Ecuador	South America	2009	M. Ramirez	KF929073	—
Onopidae	Orchestiminae	<i>Orchestina</i>	Sum1	F	250	30872	Ecuador	South America	2009	M. Ramirez	KF929074	—
Onopidae	Orchestiminae	<i>Orchestina</i>	sp.	M	399	16995	Singapore	Asia	2012	P. Grootaert / A. Henrard	KF929042	—
Onopidae	Orchestiminae	<i>Orchestina</i>	sp.	M	241	14882	Argentina	South America	2008	M. Ramirez	KF929055	KF929146
Onopidae	Orchestiminae	<i>Orchestina</i>	sp.	F	137	14909	Argentina	South America	2009	M. Ramirez	KF929054	—
Onopidae	Orchestiminae	<i>Orchestina</i>	sp.	M	393	16990	Singapore	Asia	2012	P. Grootaert / A. Henrard	KF929043	—
Onopidae	Sulsulinae	<i>Puan</i>	<i>chechehet</i>	M	412	43348	Chile	South America	2010	N. Ferretti	KF929023	KF929136
Onopidae	Sulsulinae	<i>Unicorn</i>	sp.	F	415	42236	Chile	South America	2010	M. Izquierdo	KF929024	—
Onopidae	Sulsulinae	<i>Unicorn</i>	<i>catleyi</i>	M	245	15059	Argentina	South America	2006	M. Ramirez	KF929025	KF929135
Orsolobidae		<i>Duripelta</i>	<i>borealis</i>	—	145	10375	New Zealand	Oceania	2005	B. Baehr	KF929035	—

Table 1 continued.

Orsolobidae	<i>Orsolobus</i>	<i>pucara</i>	M	416	—	Chile	South America	—	M. Izquierdo	KF929026	KF929137
Segestrinae	<i>Ariadna</i>	<i>araucana</i>	F	304	—	Chile	South America	2009	M. Ramirez	KF929027	KF929140
Segestrinae	<i>Ariadna</i>	<i>maxima</i>	—	106	—	Chile	South America	2008	M. Ramirez	KF929029	KF929141
Segestrinae	<i>Ariadna</i>	<i>boesenbergi</i>	F	307	—	Argentina	South America	2010	M. Ramirez	KF929028	—
Segestrinae	<i>Segestria</i>	<i>florentina</i>	F	305	—	Argentina	South America	2010	M. Ramirez	KF929036	—
Segestrinae	<i>Segestria</i>	sp.	—	—	—	Spain	Europe	—	(BIDGARAY-BATISTA & ARNEO 2011)	JN689079	—
Dysderidae	<i>Harpactocrates</i>	<i>troglophilus</i>	—	—	—	Turkey	Europe	—	(BIDGARAY-BATISTA & ARNEO 2011)	JN689046	—
Dysderidae	<i>Dysdera</i>	<i>crocata</i>	F	199	—	Portugal	Europe	2010	A. Henriard	KF929031	—
Dysderidae	<i>Dysdera</i>	<i>silvatica</i>	—	—	—	Canary Islands	Europe	—	(BIDGARAY-BATISTA & ARNEO 2011)	JN689050	—
Dysderidae	<i>Dysdera</i>	<i>enythina</i>	—	180	—	Belgium	Europe	—	R. Jocqué	KF929034	—
Dysderidae	<i>Harpactea</i>	<i>homborgi</i>	M	86	—	Belgium	Europe	2008	R. Jocqué	KF929033	KF929139
Dysderidae	<i>Harpactea</i>	<i>homborgi</i>	F	303	—	France	Europe	2004	M. Ramirez	KF929032	KF929138
Dysderidae	<i>Parachites</i>	<i>teruelis</i>	—	—	—	Spain	Europe	—	(BIDGARAY-BATISTA & ARNEO 2011)	JN689087	—
Trogloraptoridae	<i>Trogloraptor</i>	sp.	juv.	391	—	USA	North America	2012	P. Jäger	KF929030	KF929194
Filistidae	<i>Kukulcania</i>	<i>hibernalis</i>	—	—	—	—	—	—	(WOOD et al. 2012)	JX240253	—
Filistidae	<i>Pritha</i>	<i>cf. pallida</i>	M	417	—	France	Europe	2012	A. Henriard	KF929037	KF929192
Liphistiidae	<i>Liphistius</i>	sp.	—	—	—	Malaysia	Asia	—	(HEDIN & BOND 2006)	DD639767	—

the saved trees. Bootstrap support values were obtained with 1000 bootstrap replicates (time limit set to 60 s per bootstrap replicate). BI analyses were performed using MrBayes ver. 3.2.1 (RONQUIST & HUELSENBECK 2003) available on the University of Oslo Bioportal computer cluster (KUMAR et al. 2009, <http://www.bioportal.uio.no>). In a first setup, both 18S, 28S and the 18S-28S alignments were analysed under a general time reversible (GTR; YANG 1994) model with all model parameters estimated from the data, a gamma distribution to account for site rate variation (+G) and a proportion of invariant sites (+I) as selected by jModeltest (POSADA 2008). In the second setup, a mixed model was applied to the structural 18S alignment. The mixed model takes into account the secondary structure by modelling the RNA paired (stem) regions separately from unpaired (loop) regions. The stem regions in which nucleotide pairing results in strong correlation of substitutions across sites, were modelled by the doublet model and a 4 × 4 model (GTR+I+G) was used for the loop regions. All analyses were run with two different Metropolis-coupled Markov chains (MCMC, four chains) for 10 million generations with sampling every 1000th generation. To ensure that MCMC convergence was reached, we evaluated the average standard deviations of split frequencies (ASDSF), the potential scale reduction factors (PSRF) and the plots of likelihood versus generation. 25% of the trees were discarded as burn-in and posterior probabilities were calculated from the remnant set of trees. ML analyses were performed using the program RAXMLGUI 1.3. (SILVESTRO & MICHALAK 2012). The GTR model with a gamma distributed rate of variation across sites was implemented for the 18S MAFFT alignment, 28S alignment and the concatenated data set. A mixed RNA/DNA model setup (RNA6A) was used to conduct the ML tree reconstruction for the 18S structural alignment. The best scoring tree (with the highest likelihood score out of 100 heuristic searches starting from distinct randomized maximum parsimony starting trees) is visualised with bootstrap values calculated from 1000 pseudo-replicates.

3. Results

3.1. rRNA sequences

The most successful amplification results were obtained for the 18S ribosomal gene fragment. More precisely 120 taxa representing 36 oonopid genera were obtained. The amplified fragment is on average 1630 nt long and has an average GC content of 50%. 92 positions representing five loop regions were highly variable and excluded from the phylogenetic analyses. The 18S MAFFT alignment comprised 1781 positions of which 689 were variable

(540 parsimony informative sites). The 18S structural alignment comprised 1801 positions of which 703 were variable (551 parsimony informative sites). The average level of intraspecific 18S sequence variation was 0.18% (calculated for *Paradysderina vlad* Platnick & Dupérré, 2011, *Neotrops waorani* Grismado & Ramirez, 2013, *Heteroonops spinimanus* Platnick & Dupérré, 2009, *Orchestina communis* Henrard & Jocqué, 2012, *Tapinesthis inermis* and *Brignolia kapit* Platnick et al., 2011). Intrageneric 18S sequence variation within 20 oonopid genera was on average 1.8%, which was much higher than within one dysderid genus (*Dysdera* Latreille, 1804: 0.5%) and the two segestriid genera (*Segestria* Latreille, 1804: 0.6%, *Ariadna* Audouin, 1826: 0.2%) (El. Suppl. Table S1). In general, 18S sequence variation across all oonopid specimens was high (average 6.4%, El. Suppl. Table S1). The 28S-rRNA dataset contained 64 taxa representing 27 oonopid genera. Gblocks eliminated 13% of the 28S alignment resulting in a partial 28S fragment, which was on average 959 nt long and had an average GC content of 59%. Intraspecific (calculated for *Neotrops waorani*, *Tapinesthis inermis*, *Brignolia kapit*) and intrageneric variation was on average 0.2% and 5.3% respectively (El. Suppl. Table S1). The 28S alignment comprised 974 positions, of which 497 were variable (421 parsimony informative sites). The combined 18S-28S dataset contained 57 taxa (27 oonopid genera) and 2752 characters of which 1024 were variable (801 parsimony informative).

3.2. Molecular phylogenetics

Evolutionary history was reconstructed by means of BI, ML and MP carried out on the structural and MAFFT 18S alignment (Fig. 2), 28S alignment (El. Suppl. Fig. S1) and the combined 18S-28S alignment (Fig. 3). For each of these different alignments, all three analysis types (*i.e.* BI, ML and MP) resolved consistently similar clades of species groups within the Oonopidae, however, the degree of resolution varied with BI analyses tending toward more resolution and MP analyses toward less. Higher-level relationships were more difficult to resolve based on each gene separately. In contrast, different analysis types on the combined 18S-28S alignment resolved consistently the same higher-level relationships.

One possible drawback of ribosomal DNA genes is the possibility of amplification of paralogous copies which might confound phylogenetic reconstruction (MURPHY et al. 2006; VINK 2013; VINK et al. 2011). The consistent phylogenetic results among the two rRNA-gene trees, the absence of uninterpretable sequence chromatograms, the absence of multiple PCR bands and of long-branch attraction currently suggest no indication of the presence of paralogous copies in these datasets. Nonetheless, the possibility of paralogy should still be kept in mind and future comparison with additional genes is encouraged.

3.2.1. Oonopidae

The monophyly of the Oonopidae was consistently strongly supported by analysis of the 28S alignment (1.00 Posterior Probability (PP), 54.6 ML, 93 MP, El. Suppl. Fig. S1) and the combined 18S-28S alignment (1.00 PP, 96 ML, 70.5 MP, Fig. 3). The latter is in contrast with the less consistent results based on the 18S alignments, which contained a higher number of oonopid genera (37 versus 27). Within all analyses based on both structural and MAFFT 18S alignments, monophyly of Oonopidae was not recovered. However, BI analyses consistently produced trees with a well-supported polytomous clade containing all taxa representing Oonopidae, Dysderidae and Orsolobidae (Fig. 2). Within this clade the majority of the Oonopidae genera were recovered as a monophyletic group but with weak support (MAFFT: 0.72 PP, Structural: 0.63 PP), Dysderidae monophyly was robustly supported (PP= 1) while in contrast the orsolobids (*Orsolobus* Simon, 1893 and *Duripelta* Forster, 1956) were not monophyletic and varied in their phylogenetic position depending on the type of alignment and the analysis type. The latter was also observed for a small set of soft-bodied oonopid genera (*Birabenella*, *Heteroonops* and *Oonopoides*) and the genus *Stenoonops* Simon, 1891. More precisely, the BI based on the structural 18S alignment taking into account the secondary structure reconstructs a tree in which the genera *Birabenella*, *Heteroonops* and *Oonopoides* are monophyletic (0.97 PP) and placed as a sister clade of *Orsolobus pucara* Forster & Platnick, 1985 although with very weak support (0.54 PP, Fig. 2). The BI based on the MAFFT 18S alignment placed *Heteroonops* and *Oonopoides* within a well-supported clade containing the majority of the Oonopidae (0.96 PP) while *Birabenella* and *Stenoonops* were placed more as a sister clade of *Duripelta borealis* (tree not shown). The phylogenetic position of *Heteroonops* and *Oonopoides* within a well-supported clade containing the majority of the Oonopidae is also recovered in the 28S phylogeny (El. Suppl. Fig. S1).

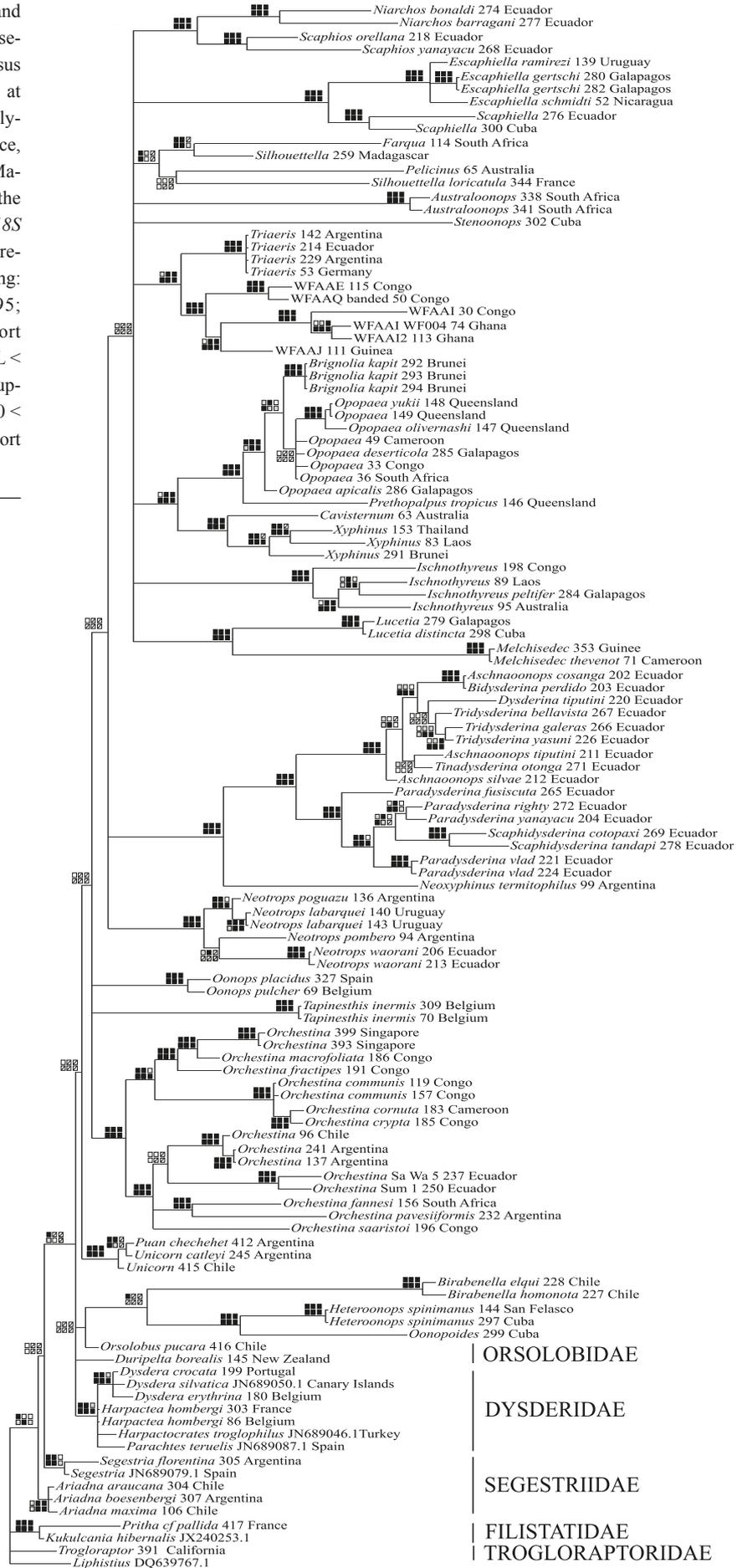
3.2.2. Intrafamilial relationships in Oonopidae

Almost all oonopid genera of which more than one specimen was included in the analyses were recovered consistently as monophyletic although five exceptions are observed, *i.e.* specimens of the genera *Silhouettella* Benoit, 1979, *Opopaea* Simon, 1891, *Paradysderina*, *Aschnaonops* and *Unicorn*. The genus *Orchestina* is well represented in the 18S analysis by 16 specimens sampled at different continental regions. Within this genus two well-supported clades are observed. Within the first clade two specimens sampled in Asia (Singapore) form a distinct group separated from specimens from Africa (Congo & Cameroon). The second clade contains specimens sampled in Africa (Congo & South Africa) and South America (Argentina, Chile & Ecuador). Interestingly, *O. pavesiiformis* Saaristo, 2007 sam-

Fig. 2. Phylogeny of Oonopidae and related families based on the *I8S* sequence data. Majority rule consensus Bayesian tree is shown. Squares at nodes indicate per column the analysis method (BI: Bayesian Inference, ML: Maximum Likelihood, MP: Maximum Parsimony) and per line the type of alignment (*I8S* structural, *I8S* MAFFT). Colours of squares represent bootstrap values as following: strong support (black: BI ≥ 0.95; ML, MP ≥ 0.70), moderate support (grey: 0.75 ≤ BI < 0.95; 0.60 ≤ ML < 0.70; 0.50 < MP < 0.70), weak support (white: 0.50 < BI < 0.75; 0.50 < MP, ML < 0.60) and no support (square with diagonal line).

BI ML MP

 I8S-structural
 I8S-MAFFT
 0.05 expected changes per site



OONOPIDAE

ORSOLOBIDAE

DYSDERIDAE

SEGESTRIIDAE

FILISTATIDAE

TROGLORAPTORIDAE

pled in Argentina is more similar in its *18S* sequence to *O. fannesi* Henrard & Jocqué, 2012 stemming from South Africa than to *Orchestina* specimens sampled in South America. The genus *Opopaea* is also represented by several specimens (7) stemming from different sampling locations. Within *Opopaea*, specimens from Australia (Queensland) form a well-supported group clearly differentiated from the remaining specimens sampled in Africa and the Galápagos that are, in contrast, very similar in *18S* sequences. *18S* sequences from different specimens of *Triaeris* Simon, 1891 sampled at different locations show no variation.

A number of genus groups within the Oonopidae are consistently resolved across genes and analysis types (Figs. 2–4). Several of these genus groups are congruent with currently defined morphological groups. More precisely we found strong support for the monophyly of the following groups: 1) all specimens of the *Dysderina*-group, 2) the two *Sulsulinae* genera, 3) *Opopaea* and *Brignolia*, 4) *Cavisternum* Baehr, Harvey & Smith, 2010 and *Xyphinus* Simon, 1893 and 5) *Heteroonops* and *Oonopoides* across both genes. Based on *18S* topologies containing most taxa, we found strong support for the monophyly of the following groups: 1) all specimens belonging to the *Zyngoonops*-group and specimens of *Triaeris*, 2) genera belonging to the *Pelycinus*-group, 3) *Lucetia* Dumitrescu & Georgescu, 1983 and *Melchisedec* Fannes, 2010 and 4) a clade including *Opopaea*, *Brignolia*, *Prethopalpus* Baehr et al., 2012, *Cavisternum* and *Xyphinus*. In contrast, specimens of the *Scaphiella*-group were not recovered as monophyletic but as two distinct monophyletic groups including 1) *Niarchos* Platnick & Dupérré, 2010 and *Scaphios* Platnick & Dupérré, 2010 and 2) *Escaphiella* Platnick & Dupérré, 2009 and *Scaphiella* Simon, 1891 respectively. A clear distinction between armoured versus soft-bodied Oonopidae was not recovered. However, soft-bodied Oonopidae were placed more basal within the Oonopidae.

3.2.3. Higher-level relationships

This study allows a preliminary insight in the phylogenetic relationships among families currently placed within the superfamily of the Dysderoidea. Across all alignments, monophyly of Dysderoidea sensu GRISWOLD et al. (2012) is not recovered. However, we found strong support for the monophyly of a group containing Oonopidae, Orsolobidae, Segestriidae and Dysderidae based on the *18S* dataset (Fig. 2) and for a clade containing Oonopidae, Orsolobidae and Dysderidae based on the *28S* and concatenated datasets (Fig. 3, El. Suppl. Fig. S1). The monophyly of Dysderidae is supported across genes and analysis types. In contrast, neither Segestriidae nor Orsolobidae were found to be monophyletic based on the current data sets. Moreover, our phylogenies do not support a placement of Trogloraptoridae within the Dysderoidea (Figs. 2, 3, El. Suppl. Fig. S1).

4. Discussion

4.1. Monophyly and internal phylogeny of the Oonopidae

28S and combined *18S-28S* data support the hypothesis that Oonopidae are monophyletic. Similarly, *18S* weakly supports a clade containing the majority of the oonopid genera with exception of four genera. One of these genera is the soft-bodied genus *Birabenella* which is consistently placed outside the clade containing the majority of the Oonopidae genera across the type of alignment used in the BI. In contrast, the phylogenetic position of *Heteroonops*, *Oonopoides* and *Stenoonops* varies across the type of alignment used in the BI. For *Heteroonops* and *Oonopoides* a similar phylogenetic position in the *28S* phylogeny in comparison with the BI based on the *18S* MAFFT alignment was observed supporting the position of both genera within a clade containing the majority of the Oonopidae (El. Suppl. Fig. S1). Regrettably, no *28S* sequences were obtained for *Birabenella* and *Stenoonops* excluding the comparison with the *18S* results. However, it is interesting to note that *Birabenella*'s phylogenetic position is in agreement with its plesiomorphic traits such as unipectinate claws and visible seminal ducts (GRISMADO 2010).

When SIMON (1890) established the family of the Oonopidae, he classified the genera based upon the degree of body sclerotisation into either armoured “loricati”, with abdominal scuta, or soft-bodied “molles” lacking scuta (SIMON 1890). Recent work states that the soft-bodied oonopids almost certainly are not monophyletic (PLATNICK & DUPÉRRÉ 2010b; PLATNICK et al. 2012), while in contrast, PLATNICK et al. (2012) suggested that armoured oonopids might constitute a monophyletic group. Although both *18S* and *28S* topologies do not support the monophyly of these informal morphological groups, it is interesting to note that most soft-bodied genera included in this study were placed more basal within the Oonopidae. This phylogenetic pattern supports a low degree of body sclerotisation as a plesiomorphic trait while a higher degree of body sclerotisation seems a derived trait among Oonopidae. Moreover, the *28S* results are in agreement with previous work that hypothesized that *Orchestina* and the *Sulsulinae* are among the most primitive oonopids (PLATNICK et al. 2012).

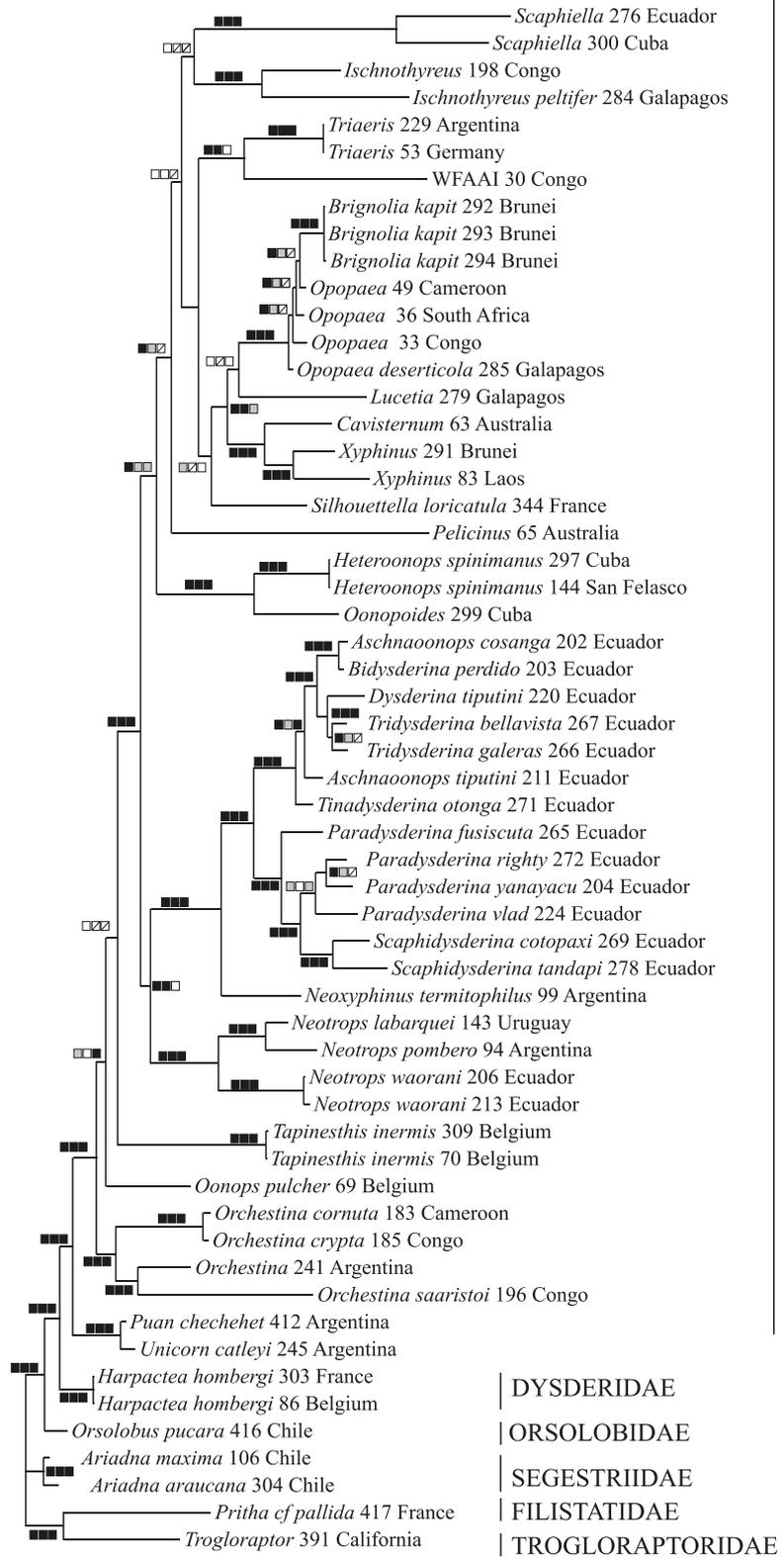
4.1.1. Orchestininae

Within this study the subfamilies *Sulsulinae* and *Orchestininae* are well supported. Interestingly, Afrotropical *Orchestina* species are not recovered as a monophyletic group. However, it should be noted that this is the first analysis that includes *Orchestina* members of different continents, something that was not tested in the phy-

Fig. 3. Phylogeny of Oonopidae and related families based on the concatenated 28S and 18S sequence data. Majority rule consensus Bayesian tree is shown. Squares at nodes indicate the analysis method (BI: Bayesian Inference, ML: Maximum Likelihood, MP: Maximum Parsimony). Colours of squares represent bootstrap values as following: strong support (black: BI ≥ 0.95; ML, MP ≥ 0.70), moderate support (grey: 0.75 ≤ BI < 0.95; 0.60 ≤ ML < 0.70; 0.50 < MP < 0.70), weak support (white: 0.50 < BI < 0.75; 0.50 < MP, ML < 0.60) and no support (square with diagonal line).

BI ML MP

0.2 expected changes per site



logeny of HENRARD & JOCQUÉ (2012). Within a first clade, Asian species studied here are placed together with Afro-tropical species belonging to the *macrofoliata*-group as defined by HENRARD & JOCQUÉ (2012). Personal observations (HA) of these (undescribed) Asian species confirm the presence of modified labial setae that are characteristic for the *macrofoliata*-group (HENRARD & JOCQUÉ 2012).

Other known Asian species – e.g. *Orchestina truncatula* (TONG & LI 2011), *O. justini* (SAARISTO 2001) – also appear to have these special setae on the labium as well as other characters diagnostic of the *macrofoliata*-group. Furthermore, the results remarkably support two sub-groups within the *macrofoliata*-group (cf. “brown clade” and “orange clade”, see HENRARD & JOCQUÉ 2012).

Although the *macrofoliata*-group is not supported as an exclusively African clade, the concept of the group by itself is still well supported by particular characters that are not present in the South American members and by the current results of the molecular data. The second clade contains both South American species and Afrotropical species. These species share the presence of a posterior plate-shaped sclerite in the female genitalia (see BURGER et al. 2010), a character that typifies to some species of the *probosciformis*-group. However, the African group in this clade, represented here only by *O. fannesi* and *O. saaristoi* (members of the “green group” in HENRARD & JOCQUÉ 2012) is perhaps the more ambiguous of all, given the low support obtained by HENRARD & JOCQUÉ (2012) and because it shares some of its own characters with many other species of the world. This idea is supported by the molecular analysis in which the South American species seem to emerge as a related group of that African clade. Interestingly, *O. fannesi* (known from South Africa) appears to be more similar to *O. pavesiiformis* (from Argentina, probably introduced from Europe, unpublished data) in *18S* sequence variation than to *O. saaristoi*. These results are in agreement with HENRARD & JOCQUÉ (2012) who concluded that the position of *O. saaristoi* within the clade containing *O. fannesi* and *O. lanceolata* Henrard & Jocqué, 2012 was questionable. In addition, *O. fannesi* and *O. pavesiiformis* (pers. obs. HA) share the type of male palpal tibia that is less strongly swollen than that of *O. saaristoi* as well as the two bristles emerging from a tubular projection near the anterior margin of the labium (HENRARD & JOCQUÉ 2012). The SEM illustrations of SAARISTO & MARUSIK (2004), corroborated by own observations (HA), show similar structures for *O. pavesii* that are clearly absent in *O. saaristoi*. In conclusion, this group of species seems to be more heterogeneous than those from *macrofoliata*, with some widespread characters that seem to be not exclusive of a particular fauna. In contrast, the *macrofoliata*-group seems to be a more homogeneous group that shares several conspicuous morphological characters restricted to some species from Africa and South Asia. However, future studies on the genus *Orchestina* from other regions (e.g. Europe, Australia) should test this hypothesis.

4.1.2. The *Dysderina*-group

The monophyly of the *Dysderina*-group is corroborated, and *Neoxyphinus* Birabén, 1953 is recovered as sister to a clade with all other taxa in the *Dysderina*-group. The other genera are divided in two clades, one comprising *Paradysderina* and *Scaphidysderina* Platnick & Dupérré, 2011, the other comprising *Dysderina* and its allies (*Aschnaonops*, *Bidysderina* Platnick et al., 2013, *Tridysderina* Platnick, Berniker & Bonaldo, 2013, and *Tinadysderina* Platnick, Berniker & Bonaldo, 2013; Figs. 2, 3). The close relationship between *Paradysderina* and *Scaphidysderina* is not surprising. These genera share an unusual instance of sexual dimorphism: in males the dor-

sal abdominal scutum is large, but in females it is greatly reduced or absent (PLATNICK & DUPÉRRÉ 2011a,b; the genus *Semidysderina* Platnick & Dupérré, 2011, not included in this study, shows a similar sexual dimorphism). In our analysis, *Paradysderina* is paraphyletic with respect to *Scaphidysderina*, suggesting that these generic names may be synonyms. However, more extensive phylogenetic studies are needed before any firm conclusion can be drawn. In most *Paradysderina* and *Scaphidysderina* species, the females lack any trace of a dorsal scutum. However, females of *P. fusiscuta* Platnick & Dupérré, 2011 and *S. scutata* Platnick & Dupérré, 2011 appear to have a small dorsal scutum at the anterior part of the abdomen (PLATNICK & DUPÉRRÉ 2011a,b). Interestingly, our study casts doubt on the monophyly of *Aschnaonops*. This genus contains 40 species and is widely distributed in northern South America and the West Indies (PLATNICK et al. 2013). The present analysis includes only three species of *Aschnaonops*, all from Ecuador, but even this small, geographically restricted sample is not recovered as monophyletic (Fig. 2). On the basis of similarities in male genital morphology, PLATNICK et al. (2013) have suggested that *Bidysderina* is more closely related to *Dysderina* than to *Aschnaonops*. However, in the present analysis, *B. perdido* is closer to *A. cosanga* than to *D. tiputini* (Figs. 2, 3).

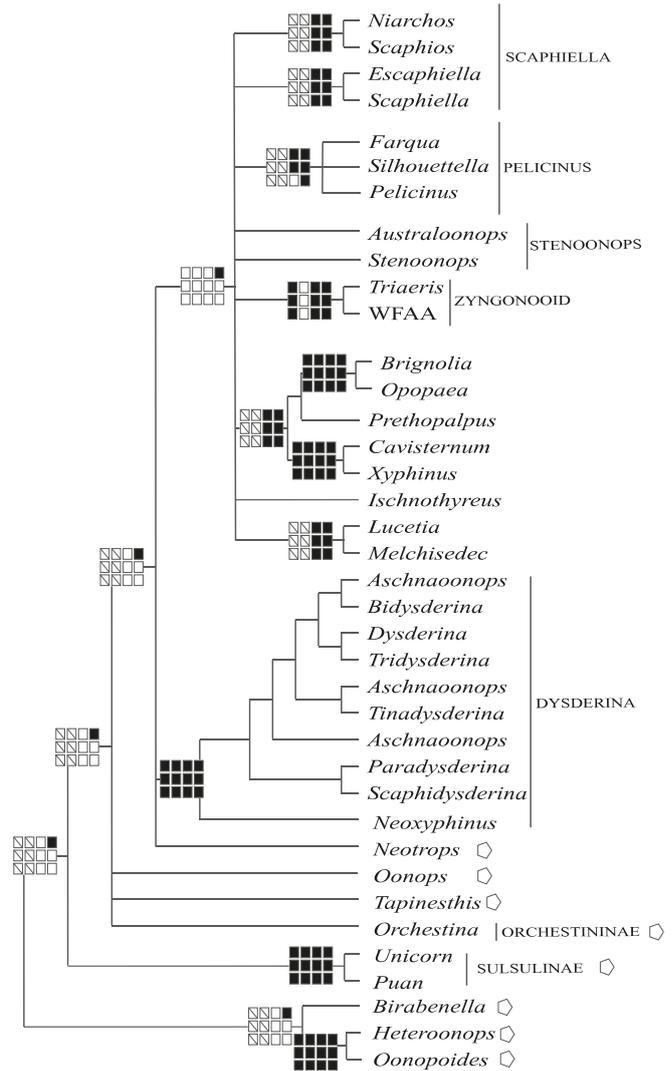
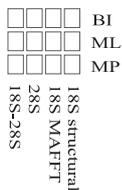
4.1.3. The *Zyngoonops*-, *Pelycinus*-, *Scaphiella*-, and *Stenoonops*-groups

The *Zyngoonops*-group is strongly supported in both the *18S* and concatenated analyses, not surprising, given that there is considerable morphological evidence for monophyly (FANNES 2013). The monophyly of the *Pelycinus*-group is supported by the *18S* data, but in the concatenated analysis the genera *Pelycinus* and *Silhouettella* are not placed as sister taxa (Fig. 3). Our current data provide little support for the *Scaphiella*-group. The proposed sister relationship between *Scaphiella* and *Escaphiella* (PLATNICK & DUPÉRRÉ 2009a) is confirmed, as is the sister relationship between *Niarchos* and *Scaphios* (PLATNICK & DUPÉRRÉ 2010a), but the four genera are not recovered as a clade (Fig. 2). Future inclusion of the remaining genera (*Pescennina* and *Simlops*) may improve the support for the *Scaphiella*-group. The *Stenoonops*-group is represented in this study by *Stenoonops* and *Australoonops* which were not recovered as sister taxa (Fig. 2). PLATNICK & DUPÉRRÉ (2010b) hypothesized a close relationship between these genera, but as only a few species could be examined by scanning electron microscopy, they cautioned that ‘this hypothesis remains poorly tested’.

4.1.4. The *Opopaea*-group

The genus *Opopaea* is one of the most species rich and widely distributed oonopid genera (PLATNICK & DUPÉRRÉ 2009b). Males of *Opopaea* have a greatly enlarged pal-

Fig. 4. Summary phylogeny of Oonopidae highlighting congruence among morphological group annotations, sequence data and inferences. Topology is based on majority rule Bayesian consensus tree of 18S-RNA structural alignment. Squares at nodes indicate per column the data partition (18S structural, 18S MAFFT, 28S, 18S-28S alignment) and per line the analysis method (BI: Bayesian Inference, ML: Maximum Likelihood, MP: Maximum Parsimony). Black squares indicate that the clade was recovered in the majority rule consensus tree of the given analysis, white squares indicate that the clade was not recovered and squares with diagonal line indicate that the clade was not tested due to missing sequence data for one or fewer taxa from the clade. Taxa with diamonds are classified as soft-bodied Oonopidae. WFAA refers to the undescribed genera belonging to the *Zyngoonops*-group.



pal patella that originates subbasally or medially from the femur (PLATNICK & DUPÉRRÉ 2009b; BAEHR 2011; BAEHR et al. 2013). Males of *Prethopalpus*, *Malagiella* and *Camptoscaphiella* (the latter two are not included in this study) share this feature with *Opopaea*. Females of *Opopaea* can be morphologically confused with members of the genera *Brignolia*. Hence, it is not surprising that both 18S and 28S topologies recovered a strong monophyletic support for *Opopaea* and *Brignolia* and that a well-supported clade consisting of *Brignolia*, *Opopaea*, and *Prethopalpus* was recovered in the 18S phylogeny.

4.2. Dysderoidea

Our dataset allows us to obtain preliminary insights into the higher-level phylogenetic relationships within the superfamily of the Dysderoidea consisting of the Oonopidae, Orsolobidae, Segestriidae and Dysderidae. The recently described family Trogloraptoridae has been suggested to be a member of the Dysderoidea (GRISWOLD et

al. 2012). Nevertheless although our results should be interpreted with caution given the relatively modest taxon sampling, our sequence data do not support a placement of Trogloraptoridae within the Dysderoidea as proposed by GRISWOLD et al. (2012). In contrast we found good support for the grouping of the Oonopidae, Orsolobidae, Segestriidae and Dysderidae thus excluding Trogloraptoridae from this natural group.

5. Conclusion

This study reports the first sequence data and most comprehensive phylogeny including a wide array of oonopid genera in combination with representatives of the superfamily Dysderoidea. At present we suggest that the majority of the oonopid genera constitute a natural group and we highlight the need for future inclusion of remaining genera before drawing firm conclusions on the

monophyly of this family. We found good support for the two subfamilies Orchestinae and Sulsulinae and several morphologically defined groups such as the *Dysderina*- and *Zyngoonops*-groups. In contrast, the *Pelicanus*-, *Stenoconops*- and *Scaphiella*-groups were not supported although future inclusion of the remaining genera of these groups might improve our understanding. We suggest that a low degree of body sclerotisation might be considered as a plesiomorphic trait and corroborate that soft-bodied Oonopidae such as *Orchestina* and Sulsulinae are relatively primitive oonopids. Additionally, the obtained phylogenies do not support a placement of the Trogloraptoridae within the superfamily of the Dysderoidea.

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7. References

- AGNARSSON I., CODDINGTON J.A., KUNTNER M. 2013. Systematics – progress in the study of spider diversity and evolution. Pp. 58–111 in: PENNEY D. (ed.), *Spider research in the 21st Century. Trends & Perspectives*. – Manchester, UK, Siri Scientific Press.
- ÁLVAREZ-PADILLA F., UBICK D., GRISWOLD C.E. 2012. *Noideattella* and *Tolegnaro*, two new genera of goblin spiders from Madagascar, with comments on the gamasomorphoid and silhouette oonopids (Araneae, Oonopidae). – *American Museum Novitates* **3745**: 1–76.
- ANDRIAMALALA D., HORMIGA G. 2013. Systematics of the goblin spider genus *Opopaea* (Araneae, Oonopidae) in Madagascar. – *Bulletin of the American Museum of Natural History* **380**: 1–156.
- BAEHR B.C. 2011. Australian goblin spiders of the genus *Opopaea* Simon, part 1. The species of the IBISCA-Queensland Project at Lamington National Park (Araneae: Oonopidae). – *Memoirs of the Queensland Museum* **55**(2): 413–437.
- BAEHR B.C., HARVEY M.S., SMITH H.M., OTT R. 2013. The goblin spider genus *Opopaea* in Australia and the Pacific islands (Araneae: Oonopidae). – *Memoirs of the Queensland Museum* **58**: 107–338.
- BIDEGARAY-BATISTA L., ARNEDO M.A. 2011. Gone with the plate: the opening of the Western Mediterranean basin drove the diversification of ground-dweller spiders. – *BMC Evolutionary Biology* **11**(317): 1–15.
- BURGER M. 2009. Female genitalia of goblin spiders (Arachnida: Araneae: Oonopidae): a morphological study with functional implications. – *Invertebrate Biology* **128**(4): 340–358.
- BURGER M., IZQUIERDO M.A., CARRERA P. 2010. Female genital morphology and mating behavior of *Orchestina* (Arachnida: Araneae: Oonopidae). – *Zoology* **113**: 100–109.
- BURGER M., MICHALIK P. 2010. The male genital system of goblin spiders: Evidence for the monophyly of Oonopidae (Arachnida: Araneae). – *American Museum Novitates* **3675**: 1–13.
- CASTRESANA J. 2000. Selection of conserved blocks from multiple alignments for their use in phylogenetic analysis. – *Molecular Biology and Evolution* **17**(4): 540–552.
- DEREEPER A., GUIGNON V., BLANC G., et al. 2008. Phylogeny.fr: robust phylogenetic analysis for the non-specialist. – *Nucleic Acids Research* **36**: 465–469.
- DUNLOP J.A., PENNEY D., JEKEL D. 2012. A summary list of fossil spiders and their relatives. The World Spider Catalog, version 12.5. – Online at <http://research.amnh.org/entomology/spiders/catalog/index.html>.
- FANNES W. 2012. Systematics and Phylogeny of Zyngoonoid Goblin Spiders (Araneae, Oonopidae). – Department of Biology, Leuven, KU Leuven. PhD dissertation. 279 pp.
- FANNES W. 2013. The goblin spider genus *Zyngoonops* (Araneae, Oonopidae), with notes on related taxa. – *Bulletin of the American Museum of Natural History* **379**: 117.
- FANNES W., DE BAKKER D., LOOSVELDT K., JOCQUÉ R. 2008. Estimating the diversity of arboreal oonopid spider assemblages (Araneae, Oonopidae) at Afrotropical sites. – *Journal of Arachnology* **36**(2): 322–330.
- FORSTER R.R., PLATNICK N.I. 1985. A review of the austral spider family Orsolobidae (Arachnida, Araneae), with notes on the superfamily Dysderoidea. – *Bulletin of the American Museum of Natural History* **1**: 1–230.
- GIRIBET G., CARRANZA S., BAGUÑA J., RIUTORT M., RIBERA C. 1996. First molecular evidence for the existence of a Tardigrada + Arthropoda clade. – *Molecular Biology and Evolution* **13**(1): 76–84.
- GRISMADO C.J. 2010. Description of *Birabenella*, a new genus of goblin spiders from Argentina and Chile (Araneae: Oonopidae). – *American Museum Novitates* **3693**: 1–21.
- GRISWOLD C., AUDISIO T., LEDFORD J. 2012. An extraordinary new family of spiders from caves in the Pacific Northwest (Araneae, Trogloraptoridae, new family). – *ZooKeys* **215**(0): 77–102.

- HARVEY M.S., EDWARD K.L. 2007. Three new species of cavernicolous goblin spiders (Araneae, Oonopidae) from Australia. – Records of the Western Australian Museum **24**: 9–17.
- HEDIN M., BOND J.E. 2006. Molecular phylogenetics of the spider infraorder Mygalomorphae using nuclear rRNA genes (18S and 28S): conflict and agreement with the current system of classification. – Molecular Phylogenetics and Evolution **41**(2): 454–471.
- HEDIN M.C., MADDISON W.P. 2001. A combined molecular approach to phylogeny of the jumping spider subfamily Dendryphantinae (Araneae: Salticidae). – Molecular Phylogenetics and Evolution **18**(3): 386–403.
- HENRARD A., JOCQUÉ R. 2012. An overview of Afrotropical canopy-dwelling *Orchestina* (Araneae, Oonopidae) with a wealth of remarkable sexual dimorphic characters. – Zootaxa **3281**(1): 1–104.
- JOCQUÉ R., DIPPENAAR-SCHOEMAN A.S. 2006. Spider Families of the World. – Tervuren, Musée Royal de L'Afrique Centrale. 366 pp.
- KATO H., MISAWA K., KUMA K.I., MIYATA T. 2002. MAFFT: a novel method for rapid multiple sequence alignment based on fast Fourier transform. – Nucleic Acids Research **30**(14): 3059–3066.
- KATO H., STANDLEY D.M. 2013. MAFFT Multiple Sequence Alignment Software Version 7: Improvements in performance and usability. – Molecular Biology and Evolution **30**(4): 772–780.
- KUMAR S., SKJAEVELAND A., ORR R., ENGER P., RUDEN T., MEVIK B.-H., BURKI F., BOTNEN A., SHALCHIAN-TABRIZI K. 2009. AIR: A batch-oriented web program package for construction of supermatrices ready for phylogenomic analyses. – BMC Bioinformatics **10**(1): 357.
- MALLATT J., SULLIVAN J. 1998. 28S and 18S rDNA sequences support the monophyly of lampreys and hagfishes. – Molecular Biology and Evolution **15**(12): 1706–1718.
- MURPHY N.P., FRAMENAU V.W., DONNELLAN S.C., HARVEY M.S., PARK Y., AUSTIN A.D. 2006. Phylogenetic reconstruction of the wolf spiders (Araneae: Lycosidae) using sequences from the 12S rRNA, 28S rRNA and NADH1 genes: implications for classification, biogeography, and the evolution of web building behavior. – Molecular Phylogenetics and Evolution **38**: 583–602.
- PENNEY D. 2006. Fossil oonopid spiders in Cretaceous ambers from Canada and Myanmar. – Palaeontology **49**(1): 229–235.
- PLATNICK N.I. 2006. The Goblin Spider PBI. – Online at <http://research.amnh.org/oonopidae/>.
- PLATNICK N.I. 2013. The World Spider Catalog, version 14.0. – Online at <http://research.amnh.org/iz/spiders/catalog/>.
- PLATNICK N.I., ABRAHIM N., ÁLVAREZ-PADILLA F., et al. 2012. Tarsal organ morphology and the phylogeny of goblin spiders (Araneae, Oonopidae), with notes on basal genera. – American Museum Novitates **3736**: 1–52.
- PLATNICK N.I., CODDINGTON J.A., FORSTER R.R., GRISWOLD C. 1991. Spinneret morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). – American Museum Novitates **3016**: 1–73.
- PLATNICK N.I., DUPÉRRÉ N. 2009a. The American goblin spiders of the new genus *Escaphiella* (Araneae, Oonopidae). – Bulletin of the American Museum of Natural History **328**: 1–151.
- PLATNICK N.I., DUPÉRRÉ N. 2009b. The goblin spider genera *Opopaea* and *Epectris* (Araneae, Oonopidae) in the New World. – American Museum Novitates **3649**: 1–43.
- PLATNICK N.I., DUPÉRRÉ N. 2009c. The goblin spider genus *Heteroonops* (Araneae, Oonopidae), with notes on *Oonops*. – American Museum Novitates **3672**: 1–72.
- PLATNICK N.I., DUPÉRRÉ N. 2010a. The Andean goblin spiders of the new genera *Niarchos* and *Scaphios* (Araneae, Oonopidae). – Bulletin of the American Museum of Natural History **345**: 1–120.
- PLATNICK N.I., DUPÉRRÉ N. 2010b. The goblin spider genera *Stenoonops* and *Australoonops* (Araneae, Oonopidae), with notes on related taxa. – Bulletin of the American Museum of Natural History **340**: 1–111.
- PLATNICK N.I., DUPÉRRÉ N. 2010c. The goblin spider genus *Scaphiella* (Araneae, Oonopidae). – Bulletin of the American Museum of Natural History **332**: 1–156.
- PLATNICK N.I., DUPÉRRÉ N. 2011a. The Andean goblin spiders of the new genera *Paradysderina* and *Semidysderina* (Araneae, Oonopidae). – Bulletin of the American Museum of Natural History **364**: 1–121.
- PLATNICK N.I., DUPÉRRÉ N. 2011b. The Andean goblin spiders of the new genus *Scaphidysderina* (Araneae, Oonopidae), with Notes on *Dysderina*. – American Museum Novitates **3712**: 1–51.
- PLATNICK N.I., DUPÉRRÉ N. 2011c. The goblin spider genus *Pescennina* (Araneae, Oonopidae). – American Museum Novitates **3716**: 1–64.
- PLATNICK N.I., DUPÉRRÉ N. 2012. The goblin spider genus *Costarina* (Araneae, Oonopidae), Part 1. – American Museum Novitates **3730**: 1–64.
- PLATNICK N.I., DUPÉRRÉ N., BERNIKER L., BONALDO A.B. 2013. The goblin spider genera *Prodysderina*, *Aschnaonops*, and *Bidysderina* (Araneae, Oonopidae). – Bulletin of the American Museum of Natural History **373**: 1–120.
- POSADA D. 2008. jModelTest: Phylogenetic Model Averaging. – Molecular Biology and Evolution **25**(7): 1253–1256.
- RAMÍREZ M.J. 2000. Respiratory system morphology and the phylogeny of haplogyne spiders (Araneae, Araneomorphae). – Journal of Arachnology **28**(2): 149–157.
- RONQUIST F., HUELSENBECK J.P. 2003. MrBayes 3: Bayesian phylogenetic inference under mixed models. – Bioinformatics **19**(12): 1572–1574.
- SAARISTO M.I. 2001. Dwarf hunting spiders or Oonopidae (Arachnida, Araneae) of the Seychelles. – Insect Systematics & Evolution **32**: 307–358.
- SAARISTO M.I., MARUSIK Y. 2004. *Ferchestina*, a new genus of oonopid spiders from Russian Far East (Aranei, Oonopidae). – Arthropoda Selecta **13**: 51–54.
- SAUPE E.E., PÉREZ-DE LA FUENTE R., SELDEN P.A., DELCLÓS X., TAFFOREAU P., SORIANO C. 2012. New *Orchestina* Simon, 1882 (Araneae: Oonopidae) from Cretaceous ambers of Spain and France: first spiders described using phase-contrast X-ray synchrotron microtomography. – Palaeontology **55**(1): 127–143.
- SILVESTRO D., MICHALAK I. 2012. raxmlGUI: a graphical front-end for RAxML. – Organisms Diversity & Evolution **12**(4): 335–337.
- SIMON E. 1890. Etudes arachnologiques. 22e Mémoire. XXXIV. Etude sur les arachnides de l'Yemen. – Annales de la Société Entomologique de France **6**: 77–124.
- SWOFFORD D.L. 1993. PAUP – A computer-program for phylogenetic inference using maximum parsimony. – Journal of General Physiology **102**(6): 9A.

- SWOFFORD D.L. 2002. *PAUP**: Phylogenetic Analysis Using Parsimony (* and other methods) v4.0b10. – Sunderland, Massachusetts, Sinauer Associates.
- TAMURA K., PETERSON D., PETERSON N., STECHER G., NEI M., KUMAR S. 2011. MEGA5: Molecular Evolutionary Genetics Analysis Using Maximum Likelihood, Evolutionary Distance, and Maximum Parsimony Methods. – *Molecular Biology and Evolution* **28**(10): 2731–2739.
- TONG Y., LI S. 2011. Six new *Orchestina* species from Hainan Island, China (Araneae, Oonopidae). – *Zootaxa* **3061**: 36–52.
- UBICK D. 2005. Oonopidae. Pp. 185–188 in: UBICK D., PAQUIN P., CUSHING P.E., ROTH V.D. (eds), *Spiders of North America: an identification manual*. – Keene (New Hampshire), American Arachnological Society.
- VINK C.J., DUPÉRRÉ N., MCQUILLAN B.N. 2011. The black headed jumping spider, *Trite planiceps* Simon, 1899 (Araneae: Salticidae): redescription including COI and paralogous 28S sequences. – *New Zealand Journal of Zoology* **38**: 317–331.
- VINK C.J. 2013. Is 28S and COI useful for interfamily spider phylogenetics? – Abstract Book. 19th International Congress of Arachnology, Kenting National Park, Taiwan June 23–28, 2013: 155.
- WOOD H.M., GRISWOLD C.E., GILLESPIE R.G. 2012. Phylogenetic placement of pelican spiders (Archaeidae, Araneae), with insight into evolution of the ‘neck’ and predatory behaviors of the superfamily Palpimanoidea. – *Cladistics* **28**(6): 598–626.
- YANG Z. 1994. Estimating the pattern of nucleotide substitution. – *Journal of Molecular Evolution* **39**(1): 105–111.

Electronic Supplement Files

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File: debusschere&al-oonopidaephylogeny-asp2014-electronicsupplement.pdf. – Fig. S1: Phylogeny of Oonopidae and related families based on 28S sequence data. – Table S1: Estimates of average evolutionary divergence.