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EDITORIAL

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Celebrating with the 'beetle' man: Terry Erwin's 75th birthday

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Our much respected Editor-in-Chief turns 75 years on 1st December, and we would like to seize the opportunity to thank him for all the support and wish him many more years of success and fruitful collaboration with us. Terry Erwin was with ZooKeys from the very beginning. Words can barely describe how much has he contributed to strengthening and developing the journal, especially during its infancy. ZooKeys wouldn't be what it is now without his great enthusiasm, endless care and friendly attitude to our staff (see our latest editorial Erwin T, Stoev P, Georgiev T, Penev L (2015) ZooKeys 500: traditions and innovations hand-in-hand servicing our taxonomic community). With the following short biographic note, we would like to wholeheartedly say to our god father

Thank you, Terry! We wish you a long, healthy and happy life!

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Terry L. Erwin was born in St. Helena of Napa County, California on December 1, 1940. His father was a "tin-knocker" i.e., a sheetmetal worker, and race car driver in the California circuit; his mother was a government clerk. Terry spent his youth trout fishing in the High Sierra with his maternal grandfather. As a teenager, with prodding from his father, he began building hot-rod cars and was a founding member and later the President of the California Conquistadores, a hot-rod club in the San Francisco Bay Area.

He put himself through college by working on Atomic Submarines at Mare Island Naval Shipyard where he was a helper in the "Asbestos" department. It was exactly at this time, when he made the life-changing decision that following his father's footsteps was not in the cards for him. He then became a student under the guidance of the noted Coleopterist, J. Gordon Edwards, at San Jose State College. With the help of Gordon's enthusiasm and guidance, Terry solved the intractable taxonomy of the Californian Bombardier Beetles – a group that still stays close to his heart. He then went on to explore the global bombardian beetle fauna for his dissertation under the mentorship of George E. Ball at the University of Alberta, Canada, finishing in 1969, who to this day is still his dear Mentor. And, continuing Ball's tradition of mentoringship, he has now his own Mentees, all young women working on carabid beetle projects.

Having decided that he wanted to work under the three greatest (living) carabidologists, the first being Prof. Ball, Terry obtained postdoctoral fellowships at the Museum of Comparative Zoology at Harvard with Philip J. Darlington Jr. and at Lund University, Sweden with Carl H. Lindroth. However, a position opened at the National Museum of Natural History, Smithsonian Institution (then the USNM or United States National Museum) in the Department of Entomology upon the retirement of Oscar Cartwright. With the support of Washington Biologists Field Club (WBFC) members Paul Spangler (Coleopterist) and Karl Krombien (Chairman of Entomology), Terry was able to accept the position and within two months took a year-long sabbatical to Sweden to study with Lindroth.

He returned in 1971, to take up the reins as the second Coleopterist within the Department (now he is the only Coleopterist with the Smithsonian Institution in charge of 12 million museum specimens). While in Sweden, the Chairmanship of the Department turned over from Karl Krombien to Paul D. Hurd, who upon arrival saw on his new desk a proposal previously left by Terry asking to obtain funding for studies of the California carabid beetles. Having learned of monies for studies in Central America, Hurd crossed out "California" and wrote "Panama." To Terry's great surprise, he arrived home from Sweden only to find out he was checked in on the next plane to the Canal Zone. That journey made the beginning of a lifetime career devoted to the studies of biodiversity in Neotropical forests.

In 1982, with the publication of a small paper (Erwin TL (1982) Tropical forests: Their richness in Coleoptera and other arthropod species. The Coleopterists Bulletin 36 (1): 74–75) on the beetle fauna of a Panamanian tree species, Terry created a cottage industry in canopy studies both with the fogging technique of collecting canopy arthropods, but also in trying to estimate the number of species on the planet. In that paper, he had hypothesized that there were as many as 30 million species worldwide, an

order of magnitude difference from the existing estimates at the time predicting just 1 million. A lot of people got excited, especially those in the Conservation business. If true, this meant that the world was losing a lot more species than previously imagined. The tiny 1.5-page paper that Terry wrote 34 years ago, has now been cited more than 1000 times.

Today, Terry continues his studies of biodiversity in the western Amazon Basin, at present in Ecuador. He has also not forgotten his favorite beetles, currently conducting taxonomic studies on carabids, particularly those genera living in the rainforest canopy. Being a prolific author he has written altogether (as of 20 November 2015) 270 papers, books, and monographs, most of them dealing with his favorite coleopterans. Keep up with Terry's publications on Google Scholars.

More information about Terry Erwin and his exciting career can be found in Rice ME (2015) Terry L. Erwin: She Had a Black Eye and in Her Arm She Held a Skunk. American Entomologist, volume 61, number 1, republished in ZooKeys 500: 9–24. doi: 10.3897/zookeys.500.9772.

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Table 1. List of taxa named after Terry Erwin.

Order	Family	Subfamily (1)	Genus (2)	Species (47)	Subspecies (1)	Specauthor	Specdate	Locality
Coleoptera	Carabidae		*Erwiniana*			Paulsen & Smith	2003-	Neotropics
Hymenoptera	Dryinidae	Erwininae	*Erwinius*			Olmi & Guglielmino	2010-	Ecuador
Coleoptera	Carabidae		*Abaris*	*erwini*		Will	2002-	Bolivia; Perú
Coleoptera	Carabidae		*Anaulacus*	*erwini*		Ball & Shpeley	2002-	Perú
Coleoptera	Carabidae		*Anillinus*	*erwini*		Sokolov & Carlton	2004-	USA - NC, VA
Coleoptera	Carabidae		*Bembidion*	*erwini*		Perrault	1982-	México - OA
Coleoptera	Carabidae		*Calathus*	*erwini*		Ball & Nègre	1972-	México - JA, MH
Coleoptera	Carabidae		*Carabus*	*erwini*		Mandl	1975-	
Coleoptera	Carabidae		*Catascopus*	*erwini*		Straneo	1994-	
Coleoptera	Carabidae		*Clinidium*	*erwini*		Bell & Bell	2009-	Costa Rica
Coleoptera	Carabidae		*Coptodera*	*erwini*		Shpeley & Ball	1993-	Perú
Coleoptera	Carabidae		*Ctenostoma*	*erwini*		Naviaux	1998-	Panamá
Coleoptera	Carabidae		*Ctenostoma*	*erwini*		Naviaux	1998-	Ecuador - Galápagos Islands: Baltra (Seymour), Darwin (Culpepper), Fernandina (Narborough), Floreana, Genovesa (Tower), Pinta (Abingdon), Santa Cruz (Indefatigable), Santa Fé (Barrington), Wolf (Wenman).
	Carabidae		*Dyschiriodes*	*erwini*		Bulirsch	2009-	Neotropics
Coleoptera	Carabidae		*Dyschirius*	*erwini*		Bulirsch	2009-	Argentina – Santiago del Estero
Coleoptera	Carabidae		*Geocharidius*	*erwini*		Sokolov & Kavanugh	2014-	Central America

Order	Family	Subfamily (1)	Genus (2)	Species (47)	Subspecies (1)	Specauthor	Specdate	Locality
Coleoptera	Carabidae		*Eucheila*	*erwini*		Ball and Shpeley	2001-	Perú
Coleoptera	Carabidae		*Eurycoleus*	*erwini*		Spheley & Ball	2001-	Costa Rica
Coleoptera	Carabidae		*Paratrechus*	*erwini*		Barr	1982-	México – VC
Coleoptera	Carabidae		*Tachys*	*erwini*		Reichardt	1976-	Ecuador - Galápagos Islands: Baltra (Seymour), Darwin (Culpepper), Fernandina (Narborough), Floreana, Genovesa (Tower), Pinta (Abingdon), Santa Cruz (Indefatigable), Santa Fé (Barrington), Wolf (Wenman).
Coleoptera	Carabidae		*Tetracha*	*erwini*		Naviaux	2010-	Brazil - Roraima
Coleoptera	Carabidae		*Trichopsida*	*erwini*		Larochelle & Lariviere	2013-	New Zealand
Coleoptera	Carabidae		*Phloeoxena*	*megalops*	*erwinorum*	Ball	1975-	
Coleoptera	Carabidae		*Trichopselaphus*	*erwino-rum*		Ball	1978-	Costa Rica; Panamá
Araneoidea	Araneidae		*Kaira*	*erwini*		Levi	1993-	Peru
Araneoidea	Oonopidae		*Gradunguloo-nops*	*erwini*		Grismado, Izquierdo, Gonzalez & Ramirez	2015-	Neotropics
Araneoidea	Oonopidae		*Dysderina*	*erwini*		Platnick, Berniker & Bonaldo	2013-	Neotropics
Araneoidea	Pisauridae		*Architis*	*erwini*		Santos	2007-	Neotropics
Coleoptera	Chrysomeli-dae		*Chrysomila*	*erwini*		Salvini, Escalona & /Furth	2008-	Peru

Order	Family	Subfamily (1)	Genus (2)	Species (47)	Subspecies (1)	Specauthor	Specdate	Locality
Coleoptera	Ciidae		*Phellinocis*	*erwini*		Lopes-Andrade & Lawrence	2005-	Neotropics
Coleoptera	Cleridae		*Enoclerus*	*erwini*		Ekis	1978-	Costa Rica, Panama
Coleoptera	Curculionidae		*Ceutorhynchus*	*erwini*		Korotyaev & O'Brien	2008-	USA - CA
Diptera	Aulacigastridae		*Aulacigaster*	*erwini*		Rung & Mathis	2011-	Ecuador
Diptera	Clusiidae		*Sobarocephala*	*erwini*		Londdale & Marshall	2012-	Neotropics
Diptera	Lauxaniidae		*Eurystratiomyia*	*erwini*		Gaimari & Silva	2010-	
Diptera	Tephritidae		*Molynocoelia*	*erwini*		Norrbom	2011-	Ecuador
Hemiptera	Cicadellidae		*Gabrita*	*erwini*		Nielson	2010-	Neotropics
Hemiptera	Cicadellidae		*Daedaloscarta*	*erwini*		Cavichioli & Takiya	2012-	Neotropics
Hemiptera	Cixiidae		*Loisirella*	*erwini*		Holzinger, Holzinger & Egger	2013-	Ecuador
Hemiptera	Rhyparochromidae	Rhyparochromidae	*Villalobosothignus*	*erwini*		Dellape & Montemayor	2011-	Ecuador
Hymenoptera	Aphelininae		*Punkaphytis*	*erwini*		Kim & Heraty	2012-	Neotropics
Hymenoptera	Dryinidae		*Deinodryinus*	*erwini*		Olmi	2008-	Neotropics
Hymenoptera	Eucharitidae		*Orasema*	*erwini*		Burks, Mottern & Heraty	2015-	Neotropics

Order	Family	Subfamily (1)	Genus (2)	Species (47)	Subspecies (1)	Specauthor	Specdate	Locality
Hymenoptera	Eurytomidae		*Khamul*	*erwini*		Gates	2008-	Ecuador
Hymenoptera	Ichneumonidae		*Stethantyx*	*erwini*		Townes	1971-	Neotropics
Hymenoptera	Trichogrammatidae		*Adryas*	*erwini*		Pinto & Owen	2004-	Neotropics
Psocoptera	Lachesillidae		*Waoraniella*	*erwini*		Garcia Aldrete	2006-	Ecuador
Psocoptera	Ptiloneuridae		*Loneura*	*erwini*		New & Thornton	1988-	Peru
Psocoptera	Ptiloneuridae		*Triplocania*	*erwini*		Neto, Rafael & Garcia Aldrete	2014-	Ecuador
Psocoptera	Psocidae		*Trichadenotecnum*	*erwini*		Yoshizawa, Garcia Aldrete & Mockford	2008-	Neotropics
Psocoptera	Troctopsocoidae		*Troctopsocoides*	*erwini*		Mockford & Garcia Aldrete	2014-	Peru

List of the taxa described by Terry Erwin.

Table 2. List of the tribes described by Terry Erwin.

Tribe	Tribauthor	Tribdate
Systolosomatini	Erwin	1985:467
Amarotypini	Erwin	1985:467
Loxandrini	Erwin & Sims	1984:383
Xenaroswellanini	Erwin	2007:563

Table 3. List of the genera described by Terry Erwin.

Genus	Genauthor	Gendate
Archaeocindis	Kavanaugh & Erwin	1991:359
Argentinatachoides	Sallenave, Erwin & Roig	2008:8
Bembidarenas	Erwin	1972:8
Costitachys	Erwin	1974:128
Geballusa	Erwin	1994:574
Gouleta	Erwin	1994:578
Guatemalteca	Erwin	2004:12
Guyanemorpha	Erwin	2013:14
Hybopteroides	Erwin & Ball	2012:191
Inpa	Erwin	1978:31
Manumorpha	Erwin & Geraci	2008:86
Meotachys	Erwin	1974:130
Moirainpa	Erwin	1984:512
Peruphorticus	Erwin & Zamorano	2014:26
Pseudophorticus	Erwin	2004:7
Quammenis	Erwin	2000:279
Samiriamorpha	Erwin & Geraci	2008:89
Tachysbembix	Erwin	2004:3
Tuxtlamorpha	Erwin & Geraci	2008:82
Valeriaaschero	Erwin	2004:14
Xenaroswelliana	Erwin	2007:563
Yasunimorpha	Erwin & Geraci	2008:87

Table 4. List of the species described by Terry Erwin.

Genus	Species	Specauthor	Specdate	Locality
Agra	*aeroides*	Erwin	1983:284	Brazil
Agra	*anthrax*	Erwin	1986:314	Brazil
Agra	*ariasi*	Erwin	1982:200	Brazil
Agra	*atlas*	Erwin	1984:25	Trinidad
Agra	*atriperna*	Erwin	1984:42	Costa Rica; Panamá
Agra	*azureipennis*	Erwin	1982:208	Perú; Venezuela
Agra	*belize*	Erwin	1984:41	Belize
Agra	*blumax*	Erwin	1983:283	Brazil
Agra	*cachimbo*	Erwin	1984:30	Brazil
Agra	*cadabra*	Erwin	1986:303	Ecuador
Agra	*calamitas*	Erwin	1986:314	Brazil
Agra	*caliga*	Erwin	1982:206	Panamá
Agra	*campana*	Erwin	1983:273	Costa Rica; Panamá
Agra	*cauca*	Erwin	1998:509	Colombia
Agra	*cavei*	Erwin	1984:33	Paraguay
Agra	*chapada*	Erwin	1987:148	Brazil
Agra	*chocha*	Erwin	1986:304	Guyane; Suriname; Trinidad; Venezuela
Agra	*cobra*	Erwin	1982:56	Guyana
Agra	*coleps*	Erwin	1982:52	Guyane
Agra	*constans*	Erwin	1984:28	Brazil
Agra	*cuneolus*	Erwin	1983:272	Brazil
Agra	*cyaneucnemes*	Erwin	1984:45	Colombia
Agra	*dation*	Erwin	1987:156	Brazil
Agra	*dora*	Erwin	1984:34	Perú
Agra	*dorazul*	Erwin	1984:44	Colombia
Agra	*dryas*	Erwin	1982:55	Brazil
Agra	*ecaligis*	Erwin	1982:197	Ecuador
Agra	*ega*	Erwin	1982:60	Brazil
Agra	*eowilsoni*	Erwin	1998:509	Colombia
Agra	*eucera*	Erwin	1984:21	Panamá
Agra	*eucnemes*	Erwin	1984:23	Ecuador
Agra	*falsisagax*	Erwin	1982:55	Brazil
Agra	*fortuna*	Erwin	1983:270	Costa Rica; Panamá
Agra	*goyazella*	Erwin	1984:30	Brazil
Agra	*howdenorum*	Erwin	1982:194	Trinidad
Agra	*imaginis*	Erwin	1986:306	Brazil
Agra	*inca*	Erwin	1986:307	Perú
Agra	*inpa*	Erwin	1983:282	Brazil
Agra	*invicta*	Erwin	1982:58	Brazil
Agra	*iota*	Erwin	1984:33	Perú
Agra	*iquitosana*	Erwin	1982:201	Brazil; Perú
Agra	*lata*	Erwin	1987:157	Bolivia
Agra	*limulus*	Erwin	1982:199	Ecuador; Perú
Agra	*littleorum*	Erwin	1984:28	Brazil
Agra	*luehea*	Erwin	1983:285	Panamá
Agra	*magdalena*	Erwin	1987:159	Colombia

Genus	Species	Specauthor	Specdate	Locality
Agra	*maxli*	Erwin	1982:69	Brazil
Agra	*memnon*	Erwin	1987:157	Brazil
Agra	*mniszechi*	Erwin	1982:64	Guyane
Agra	*moira*	Erwin	1983:288	Brazil
Agra	*nigrarima*	Erwin	1984:25	Trinidad
Agra	*nola*	Erwin	1986:302	Costa Rica; Ecuador; Panamá
Agra	*notichlora*	Erwin	1984:33	Paraguay
Agra	*notiocyanea*	Erwin	1984:34	Bolivia
Agra	*nox*	Erwin	1984:25	Guyane
Agra	*oiapoquensis*	Erwin	1982:53	Brazil
Agra	*orabrocha*	Erwin	1984:43	Panamá
Agra	*paloma*	Erwin	1984:39	México
Agra	*para*	Erwin	1987:152	Brazil
Agra	*pearsoni*	Erwin	1984:36	Perú
Agra	*pennyi*	Erwin	1982:64	Brazil
Agra	*perkinsorum*	Erwin	1986:298	México
Agra	*phainops*	Erwin	1986:306	Surinam; Venezuela
Agra	*phite*	Erwin	1987:149	Bolivia
Agra	*pseuderythropus*	Erwin	1982:52	Guyane
Agra	*quararibea*	Erwin	1993:25	Perú
Agra	*rhomboides*	Erwin	1982:60	Guyane
Agra	*rubra*	Erwin	1987:153	Brazil
Agra	*rufarima*	Erwin	1984:27	Trinidad
Agra	*saltatrix*	Erwin	1982:65	Perú
Agra	*saramax*	Erwin	1993:22	Bolivia; Ecuador
Agra	*sasquatch*	Erwin	1982:208	Brazil
Agra	*satipo*	Erwin	1984:34	Perú
Agra	*seabrae*	Erwin	1982:205	Brazil
Agra	*serra*	Erwin	1984:28	Brazil
Agra	*sironyx*	Erwin	1984:25	Trinidad
Agra	*sphenarion*	Erwin	1982:65	Perú
Agra	*spina*	Erwin	1983:272	Brazil
Agra	*stockwelli*	Erwin	1984:36	Panamá
Agra	*tarapoto*	Erwin	1984:30	Perú
Agra	*tarapotoana*	Erwin	1982:201	Perú
Agra	*tessera*	Erwin	1983:272	Brazil
Agra	*tingomaria*	Erwin	1984:36	Perú
Agra	*titan*	Erwin	1982:201	Brazil; Guyane
Agra	*tuitis*	Erwin	1987:156	Perú
Agra	*tumatumari*	Erwin	1982:199	Guyana
Agra	*varzeicola*	Erwin	1982:199	Brazil
Agra	*vate*	Erwin	1986:302	Costa Rica; Guatemala; México; Panamá
Agra	*vation*	Erwin	1983:287	Perú
Agra	*vesedes*	Erwin	1984:46	South America
Agra	*xingu*	Erwin	1984:28	Brazil
Agra	*yeti*	Erwin	1982:207	Brazil
Agra	*yoda*	Erwin	1982:64	Guyane

Genus	Species	Specauthor	Specdate	Locality
Agra	*zona*	Erwin	1983:282	Panamá
Agra	*demerasae*	Erwin	1984:23	Guyana
Agra	*itatiaya*	Erwin	1986:312	Brazil
Agra	*kayae*	Erwin	1984:39	Costa Rica; Belize; Guatemala; Honduras; México; Panamá
Agra	*lavernae*	Erwin	1978:265	Costa Rica; Panamá
Agra	*olivencana*	Erwin	1982:201	Brazil
Agra	*perinvicta*	Erwin	1982:56	Brazil
Agra	*yodella*	Erwin	1982:197	Guyane
Agra	*tingo*	Erwin	2000:103	Perú
Agra	*biolat*	Erwin	2000:104	Perú
Agra	*aeris*	Erwin	2000:104	Perú
Agra	*solimoes*	Erwin	2000:105	Brazil
Agra	*conhormigas*	Erwin	2000:106	Perú
Agra	*lilu*	Erwin	2000:108	Brazil
Agra	*servatorum*	Erwin	2000:110	Perú
Agra	*lindae*	Erwin	2000:111	Perú
Agra	*rondonia*	Erwin	2000:112	Brazil
Agra	*nex*	Erwin	2000:112	Brazil
Agra	*manu*	Erwin	2000:112	Perú
Agra	*dax*	Erwin	2000:115	Panamá
Agra	*orinocensis*	Erwin	2000:8	Venezuela
Agra	*novaurora*	Erwin	2000:9	Ecuador
Agra	*alinahui*	Erwin	2000:9	Ecuador
Agra	*superba*	Erwin	2000:10	Brazil; Venezuela
Agra	*maracay*	Erwin	2000:13	Venezuela
Agra	*bci*	Erwin	2000:14	Costa Rica; Panamá
Agra	*falcon*	Erwin	2000:14	Venezuela
Agra	*hovorei*	Erwin	2000:15	México
Agra	*tuxlas*	Erwin	2000:15	México
Agra	*zapotal*	Erwin	2000:15	Guatemala; México
Agra	*hespenheide*	Erwin	2000:16	Costa Rica
Agra	*paratax*	Erwin	2000:16	Costa Rica
Agra	*samiria*	Erwin	2000:16	Perú
Agra	*duckworthorum*	Erwin	2000:16	Panamá
Agra	*eponine*	Erwin	2000:16	Costa Rica
Agra	*inbio*	Erwin	2000:17	Costa Rica
Agra	*pichincha*	Erwin	2000:17	Ecuador
Agra	*othello*	Erwin	2000:19	Ecuador
Agra	*smurf*	Erwin	2000:19	Brazil
Agra	*magnifica*	Erwin	2000:19	Perú
Agra	*suprema*	Erwin	2000:20	Brazil
Agra	*yola*	Erwin	2000:282	Costa Rica
Agra	*mime*	Erwin	2000:258	Ecuador
Agra	*dable*	Erwin	2002:37	Costa Rica
Agra	*liv*	Erwin	2002:39	Costa Rica; Panamá
Agra	*santarosa*	Erwin	2002:40	Costa Rica
Agra	*solisi*	Erwin	2002:41	Costa Rica

Genus	Species	Specauthor	Specdate	Locality
Agra	*jimwappes*	Erwin	2002:16	Costa Rica
Agra	*winnie*	Erwin	2002:17	Costa Rica; El Salvador
Agra	*giesberti*	Erwin	2002:19	Costa Rica; Guatemala; Panamá
Agra	*not*	Erwin	2002:21	Costa Rica
Agra	*phallica*	Erwin	2002:22	Costa Rica
Agra	*turrialba*	Erwin	2002:24	Costa Rica
Agra	*catie*	Erwin	2002:27	Costa Rica
Agra	*fugax*	Erwin	2002:28	Costa Rica
Agra	*sirena*	Erwin	2002:29	Costa Rica
Agra	*quesada*	Erwin	2002:31	Costa Rica
Agra	*janzeni*	Erwin	2002:33	Costa Rica
Agra	*katewinsletae*	Erwin	2002:35	Costa Rica
Agra	*ubicki*	Erwin	2002:43	Costa Rica
Agra	*granodeoro*	Erwin	2002:45	Costa Rica
Agra	*schwarzeneggeri*	Erwin	2002:46	Costa Rica
Agra	*solanoi*	Erwin	2002:48	Costa Rica
Agra	*notcatie*	Erwin	2002:50	Costa Rica
Agra	*pitilla*	Erwin	2002:53	Costa Rica
Agra	*catbellae*	Erwin	2002:56	Costa Rica
Agra	*delgadoi*	Erwin	2002:58	Costa Rica; Panamá
Agra	*julie*	Erwin	2002:59	Costa Rica
Agra	*ichabod*	Erwin	2002:61	Costa Rica
Agra	*monteverde*	Erwin	2002:62	Costa Rica
Agra	*zumbado*	Erwin	2002:63	Costa Rica
Agra	*zuniga*	Erwin	2002:65	Costa Rica
Agra	*cruciaria*	Erwin	2010:6	Brazil
Agra	*grace*	Erwin	2010:7	Peru
Agra	*max*	Erwin	2010:9	Brazil
Agra	*minasianus*	Erwin	2010:10	Brazil
Agra	*notpusilla*	Erwin	2010:11	Brazil
Agra	*pseudopusilla*	Erwin	2010:13	Brazil
Agra	*ce*	Erwin	2010:16	Peru
Agra	*maia*	Erwin	2010:17	Bolivia
Agra	*piranha*	Erwin	2010:18	Ecuador
Agra	*risseri*	Erwin	2010:19	Bolivia
Agra	*tiputini*	Erwin	2010:23	Ecuador
Apotomus	*reichardti*	Erwin	1980:100	Brazil
Argentinatachoides	*balli*	Sallenave, Erwin & Roig	2008:8	Argentina
Asklepia	*campbellorum*	Zamorano & Erwin	2014:39	Brazil
Asklepia	*demiti*	Erwin & Zamorano	2014:41	Brazil
Asklepia	*duofos*	Zamorano & Erwin	2014:43	Brazil
Asklepia	*grammechrysea*	Zamorano & Erwin	2014:44	Perú

Genus	Species	Specauthor	Specdate	Locality
Asklepia	*laetitia*	Zamorano & Erwin	2014:49	Colombia
Asklepia	*matomena*	Zamorano & Erwin	2014:52	Brazil
Asklepia	*adisi*	Erwin & Zamorano	2014:55	Brazil
Asklepia	*asuncionensis*	Erwin & Zamorano	2014:57	Paraguay
Asklepia	*biolat*	Erwin & Zamorano	2014:58	Perú
Asklepia	*bracheia*	Zamorano & Erwin	2014:60	Perú
Asklepia	*cuiabaensis*	Erwin & Zamorano	2014:62	Brazil
Asklepia	*ecuadoriana*	Erwin & Zamorano	2014:64	Ecuador
Asklepia	*kathleenae*	Erwin & Zamorano	2014:66	Brazil
Asklepia	*macrops*	Erwin & Zamorano	2014:67	Argentina
Asklepia	*marchantaria*	Erwin & Zamorano	2014:69	Brazil
Asklepia	*marituba*	Zamorano & Erwin	2014:71	Brazil
Asklepia	*pakitza*	Erwin & Zamorano	2014:72	Perú
Asklepia	*paraguayensis*	Zamorano & Erwin	2014:74	Paraguay
Asklepia	*samiriaensis*	Zamorano & Erwin	2014:77	Perú
Asklepia	*stalametlitos*	Zamorano & Erwin	2014:79	Bolivia
Asklepia	*surinamensis*	Zamorano & Erwin	2014:81	Surinam
Asklepia	*vigilante*	Erwin & Zamorano	2014:85	Perú
Aspasiola	*bonita*	Erwin	2004:9	Costa Rica
Aspasiola	*osa*	Erwin	2004:14	Costa Rica
Aspasiola	*selva*	Erwin	2004:16	Costa Rica
Aspasiola	*steineri*	Erwin	2004:18	Costa Rica
Badister	*amazonus*	Erwin & Ball	2011:409	Perú
Bembidion	*palosverdes*	Kavanaugh & Erwin	1992:312	USA
Bembidion	*aeger*	Erwin	1982:475	Costa Rica
Bembidion	*armuelles*	Erwin	1982:481	Panamá
Bembidion	*barrense*	Erwin	1982:482	Panamá
Bembidion	*chiriqui*	Erwin	1982:476	Panamá

Genus	Species	Specauthor	Specdate	Locality
Bembidion	*cortes*	Erwin	1982:480	Honduras; México
Bembidion	*diabola*	Erwin	1982:473	Costa Rica
Bembidion	*edwardsi*	Erwin	1982:475	Costa Rica
Bembidion	*franiae*	Erwin	1982:479	Guatemala
Bembidion	*ixtatan*	Erwin	1982:484	Guatemala
Bembidion	*lavernae*	Erwin	1982:472	Costa Rica
Bembidion	*nahuala*	Erwin	1982:477	Guatemala
Bembidion	*purulha*	Erwin	1982:466	Guatemala
Bembidion	*quetzal*	Erwin	1982:473	Guatemala
Brachinus	*aabaaba*	Erwin	1970:161	México; USA
Brachinus	*adustipennis*	Erwin	1969:287	Costa Rica; CUBA; México; Panamá; USA
Brachinus	*alexiguus*	Erwin	1970:57	USA
Brachinus	*capnicus*	Erwin	1970:60	USA
Brachinus	*chalchihuitlicue*	Erwin	1970:79	Costa Rica; Guatemala; México; Panamá
Brachinus	*chirriador*	Erwin	1970:80	Honduras; México
Brachinus	*cibolensis*	Erwin	1970:98	México; USA
Brachinus	*cyanochroaticus*	Erwin	1969:283	Canada; USA
Brachinus	*explosus*	Erwin	1970:161	México; USA
Brachinus	*favicollis*	Erwin	1965:11	México; USA
Brachinus	*fulminatus*	Erwin	1969:288	USA
Brachinus	*galactoderus*	Erwin	1970:132	México
Brachinus	*gebhardis*	Erwin	1965:6	México
Brachinus	*ichabodopsis*	Erwin	1970:150	USA
Brachinus	*imperialensis*	Erwin	1965:17	México; USA
Brachinus	*imporcitis*	Erwin	1970:114	USA
Brachinus	*javalinopsis*	Erwin	1970:109	USA
Brachinus	*kavanaughi*	Erwin	1969:287	México; USA
Brachinus	*microamericanus*	Erwin	1969:287	USA
Brachinus	*mobilis*	Erwin	1970:159	USA
Brachinus	*oaxacensis*	Erwin	1970:117	México
Brachinus	*pallidus*	Erwin	1965:8	USA
Brachinus	*sonorous*	Erwin	1970:163	México
Brachinus	*velutinus*	Erwin	1965:17	USA
Brachinus	*vulcanoides*	Erwin	1969:287	USA
Chelonodema	*inbio*	Erwin	2000:281	Costa Rica
Coptocarpus	*philipi*	Erwin	1974:5	Australia
Coptocarpus	*chimbu*	Erwin	1974:7	New Guinea
Coptocarpus	*yorkensis*	Erwin	1974:7	Australia
Coptocarpus	*grossus*	Erwin	1974:8	Australia
Costitachys	*inusitatus*	Erwin	1974:130	Brazil; Guyane; Trinidad
Costitachys	*tena*	Erwin & Kavanaugh	2006:335	Ecuador
Epikastea	*biolat*	Erwin	2004:7	Perú
Epikastea	*grace*	Erwin	2004:13	Perú
Epikastea	*mancocapac*	Erwin	2004:15	Perú
Epikastea	*piranha*	Erwin	2004:16	Ecuador
Epikastea	*poguei*	Erwin	2004:17	Perú
Erwiniana	*aetholia*	(Erwin)	1973:12	Bolivia

Genus	Species	Specauthor	Specdate	Locality
Erwiniana	*alticola*	(Erwin)	1994:614	Colombia
Erwiniana	*am*	(Erwin)	1994:594	Perú
Erwiniana	*anchicaya*	(Erwin)	1994:607	Colombia
Erwiniana	*angustia*	(Erwin)	1994:592	Perú
Erwiniana	*anterocostis*	(Erwin)	1973:14	Costa Rica
Erwiniana	*apicisulcata*	(Erwin)	1973:18	Costa Rica
Erwiniana	*baeza*	(Erwin)	1994:582	Ecuador
Erwiniana	*batesi*	(Erwin)	1973:19	Brazil
Erwiniana	*bisulcifrons*	(Erwin)	1973:27	Brazil
Erwiniana	*chiriboga*	(Erwin)	1994:616	Ecuador
Erwiniana	*crassa*	(Erwin)	1994:583	Perú
Erwiniana	*dannyi*	(Erwin)	1994:616	Ecuador
Erwiniana	*depressisculptilis*	(Erwin)	1994:602	Ecuador
Erwiniana	*equanegrei*	(Erwin)	1994:586	Ecuador
Erwiniana	*esheje*	(Erwin)	1994:584	Perú
Erwiniana	*eugeneae*	(Erwin)	1994:605	Colombia; Perú
Erwiniana	*exigupunctata*	(Erwin)	1994:608	Brazil; Ecuador; Perú
Erwiniana	*foveosculptilis*	(Erwin)	1994:604	Brazil
Erwiniana	*grossipunctata*	(Erwin)	1973:20	Brazil
Erwiniana	*hamatilis*	(Erwin)	1994:598	Ecuador
Erwiniana	*henryi*	(Erwin)	1994:582	Ecuador
Erwiniana	*huacamayas*	(Erwin)	1994:617	Ecuador
Erwiniana	*indetecticostis*	(Erwin)	1994:595	Ecuador
Erwiniana	*iris*	(Erwin)	1973:11	Bolivia; Perú
Erwiniana	*irisculptilis*	(Erwin)	1994:603	Ecuador
Erwiniana	*jacupiranga*	(Erwin)	1994:613	Brazil
Erwiniana	*jefe*	(Erwin)	1994:608	Panamá
Erwiniana	*manusculptilis*	(Erwin)	1994:586	Perú
Erwiniana	*misahualli*	(Erwin)	1994:602	Ecuador
Erwiniana	*negrei*	(Erwin)	1973:12	Venezuela
Erwiniana	*nigripalpis*	(Erwin)	1973:9	Panamá
Erwiniana	*notesheje*	(Erwin)	1994:584	Ecuador; Perú
Erwiniana	*notparkeri*	(Erwin)	1994:598	Colombia
Erwiniana	*nox*	(Erwin)	1994:596	Ecuador
Erwiniana	*para*	(Erwin)	1994:589	Brazil
Erwiniana	*parainsularis*	(Erwin)	1973:26	Venezuela
Erwiniana	*parapara*	(Erwin)	1994:585	Brazil
Erwiniana	*parkeri*	(Erwin)	1994:597	Perú
Erwiniana	*pfunorum*	(Erwin)	1994:600	Brazil; Ecuador; Perú
Erwiniana	*protosculptilis*	(Erwin)	1994:601	Perú
Erwiniana	*punctisculptilis*	(Erwin)	1994:605	Perú
Erwiniana	*quadrata*	(Erwin)	1994:600	Perú
Erwiniana	*rosebudae*	(Erwin)	1994:612	Bolivia; Ecuador
Erwiniana	*samiria*	(Erwin)	1994:593	Perú
Erwiniana	*seriata*	(Erwin)	1973:19	Brazil
Erwiniana	*wygo*	(Erwin)	1994:615	Colombia
Eucamaragnathus	*amapa*	Erwin & Stork	1985:440	Brazil
Eucamaragnathus	*jaws*	Erwin & Stork	1985:441	Brazil

Genus	Species	Specauthor	Specdate	Locality
Geballusa	*microtreta*	Erwin	1973:24	Costa Rica; Panamá; Perú
Geballusa	*nannotreta*	Erwin	1994:577	Brazil
Geballusa	*oligotreta*	Erwin	1994:575	Panamá
Geballusa	*polytreta*	Erwin	1973:25	Brazil
Geballusa	*rex*	Erwin	1994:576	Brazil
Geocharidius	*gimlii*	Erwin	1982:488	Guatemala
Geocharidius	*phineus*	Erwin	1982:491	Guatemala
Geocharidius	*romeoi*	Erwin	1982:488	Guatemala
Gouleta	*gentryi*	Erwin	1994:580	Perú
Gouleta	*notiophiloides*	Erwin	1973:22	Brazil; Perú
Gouleta	*spangleri*	Erwin	1973:23	Panamá
Guatemalteca	*virgen*	Erwin	2004:12	Costa Rica; Guatemala; Guyane; Perú
Halocoryza	*whiteheadiana*	Erwin	2011:7	México
Hyboptera	*apollonia*	Erwin	2004:33	Costa Rica; Panamá
Hyboptera	*auxiliadora*	Erwin	2004:35	Costa Rica; México; Panamá; USA
Hybopteroides	*biolat*	Erwin & Ball	2012:195	Perú
Hybopteroides	*karolynae*	Erwin & Ball	2012:196	Perú
Hybopteroides	*penrosei*	Erwin & Ball	2012:198	Ecuador
Inpa	*psydroides*	Erwin	1978:31	Brazil; Perú; Surinam
Leistus	*madmeridianus*	Erwin	1970:117	USA
Lionepha	*chintimini*	(Erwin & Kavanaugh)	1981:63	USA
Lionepha	*lindrothellus*	(Erwin & Kavanaugh)	1981:61	Canada; USA
Lionepha	*lummi*	(Erwin & Kavanaugh)	1981:62	Canada; USA
Loricera	*aptena*	Ball & Erwin	1969:889	México
Manumorpha	*biolat*	Erwin & Geraci	2008:86	Perú
Mizotrechus	*poirieri*	Erwin	2011:110	Guyane
Mizotrechus	*bellorum*	Erwin	2011:88	Guyane
Mizotrechus	*woldai*	Erwin	2011:112	Panamá
Mizotrechus	*belvedere*	Erwin	2011:89	Guyane
Mizotrechus	*brulei*	Erwin	2011:90	Guyane
Mizotrechus	*chontalesensis*	Erwin	2011:92	Nicaragua
Mizotrechus	*costaricensis*	Erwin	2011:94	Costa Rica
Mizotrechus	*dalensi*	Erwin	2011:95	Guyane
Mizotrechus	*edithpiafae*	Erwin	2011:97	South America
Mizotrechus	*fortunensis*	Erwin	2011:98	Panamá
Mizotrechus	*gorgona*	Erwin	2011:100	Colombia
Mizotrechus	*grossus*	Erwin	2011:101	Guyane
Mizotrechus	*jefe*	Erwin	2011:101	Panamá
Mizotrechus	*marielaforetae*	Erwin	2011:104	Guyane
Mizotrechus	*minutus*	Erwin	2011:106	Guyane
Mizotrechus	*neblinensis*	Erwin	2011:108	Guyane; Venezuela
Moirainpa	*amazona*	Erwin	1984:512	Brazil; Perú
Moriosomus	*motschulskyi*	Erwin & Moore	2007:4	Perú
Nebria	*piute*	Erwin & Ball	1972:95	USA

Genus	Species	Specauthor	Specdate	Locality
Nebria	*piute*	Erwin & Ball	1972:95	USA
Nebria	*piute*	Erwin & Ball	1972:95	USA
Paratachys	*potomaca*	Erwin	1981:152	USA
Pericompsus	*alcimus*	Erwin	1974:72	Argentina; Bolivia; Paraguay; Perú
Pericompsus	*amygdali*	Erwin	1974:66	Bolivia; Venezuela
Pericompsus	*acon*	Erwin	1974:77	Bolivia
Pericompsus	*anassa*	Erwin	1974:77	Argentina; Paraguay
Pericompsus	*bilbo*	Erwin	1974:31	Venezuela
Pericompsus	*callicalymma*	Erwin	1974:68	Argentina; Brazil
Pericompsus	*carinatus*	Erwin	1974:93	Brazil
Pericompsus	*commotes*	Erwin	1974:31	Venezuela
Pericompsus	*crossarchon*	Erwin	1974:34	Brazil
Pericompsus	*crossodmos*	Erwin	1974:35	Argentina; Brazil
Pericompsus	*crossotus*	Erwin	1974:85	Brazil; Paraguay
Pericompsus	*diabalius*	Erwin	1974:83	Colombia
Pericompsus	*dynastes*	Erwin	1974:28	Venezuela
Pericompsus	*eubothrus*	Erwin	1974:71	Brazil
Pericompsus	*gongylus*	Erwin	1974:37	México
Pericompsus	*jamcubanus*	Erwin	1974:57	Cuba; Jamaica
Pericompsus	*leechi*	Erwin	1974:46	México
Pericompsus	*leucocarenus*	Erwin	1974:34	El Salvador; México
Pericompsus	*micropegasus*	Erwin	1974:75	Bolivia
Pericompsus	*morantensis*	Erwin	1974:61	Dominican Republic; Jamaica
Pericompsus	*nonandinus*	Erwin	1974:66	Brazil
Pericompsus	*pauli*	Erwin	1974:47	El Salvador; México
Pericompsus	*pegasus*	Erwin	1974:75	Bolivia
Pericompsus	*philipi*	Erwin	1974:62	Cuba; Dominican Republic; Haiti
Pericompsus	*polychaetus*	Erwin	1974:88	Bolivia
Pericompsus	*prionomus*	Erwin	1974:63	Panamá
Pericompsus	*reticulatus*	Erwin	1974:24	Brazil; Guyana
Pericompsus	*rorschachinus*	Erwin	1974:92	Bolivia; Perú; Venezuela
Pericompsus	*sagma*	Erwin	1974:45	México
Pericompsus	*silicis*	Erwin	1974:51	Brazil; Colombia; Costa Rica; Honduras
Pericompsus	*stenocitharus*	Erwin	1974:84	Paraguay
Pericompsus	*subincisus*	Erwin	1974:70	Brazil
Pericompsus	*tetraphalarus*	Erwin	1974:68	Bolivia
Pericompsus	*tlaloc*	Erwin	1974:54	Costa Rica; México
Pericompsus	*tolype*	Erwin	1974:39	Argentina; Bolivia; Brazil; Venezuela
Peruphorticus	*gulliveri*	Erwin & Zamorano	2014:26	Ecuador; Perú
Polyderis	*antiqua*	Erwin	1971:234	México
Polyderis	*moira*	Erwin	1984:513	Brazil
Polyderis	*nympha*	Erwin	1984:515	Brazil; Perú
Polyderis	*terra*	Erwin	1984:514	Brazil
Polyderis	*ucayali*	Erwin	1984:514	Brazil; Perú
Pseudomorpha	*santarita*	Erwin & Amundson	2013:47	USA

Genus	**Species**	**Specauthor**	**Specdate**	**Locality**
Pseudomorpha	*santacruz*	Erwin & Amundson	2013:45	USA
Pseudomorpha	*patagonia*	Erwin & Amundson	2013:39	USA
Pseudomorpha	*huachinera*	Amundson & Erwin	2013:36	México; USA
Pseudomorpha	*penablanca*	Amundson & Erwin	2013:42	USA
Pseudomorpha	*pima*	Amundson & Erwin	2013:44	USA
Pseudophorticus	*puncticollis*	Erwin	2004:8	Costa Rica
Quammenis	*spectabilis*	Erwin	2000:280	Costa Rica
Samiriamorpha	*grace*	Erwin & Geraci	2008:90	Perú
Tachysbembix	*sirena*	Erwin	2004:4	Costa Rica
Tachysbembix	*wendyporrasae*	Erwin	2004:6	Costa Rica
Valeriaaschero	*flora*	Erwin	2004:15	Costa Rica; Panamá
Valeriaaschero	*nigrita*	Erwin	2004:16	Costa Rica
Xenaroswelliana	*deltaquadrant*	Erwin	2007:564	Brazil
Xystosomus	*convexus*	Erwin	1973:29	Brazil
Xystosomus	*impressifrons*	Erwin	1973:32	Brazil
Xystosomus	*laevimicans*	Erwin	1973:31	Brazil
Xystosomus	*laevis*	Erwin	1973:30	Brazil
Xystosomus	*niger*	Erwin	1973:32	Brazil
Xystosomus	*paralaevis*	Erwin	1973:30	Brazil
Xystosomus	*tholus*	Erwin	1973:34	Brazil
Yasunimorpha	*piranha*	Erwin & Geraci	2008:88	Ecuador

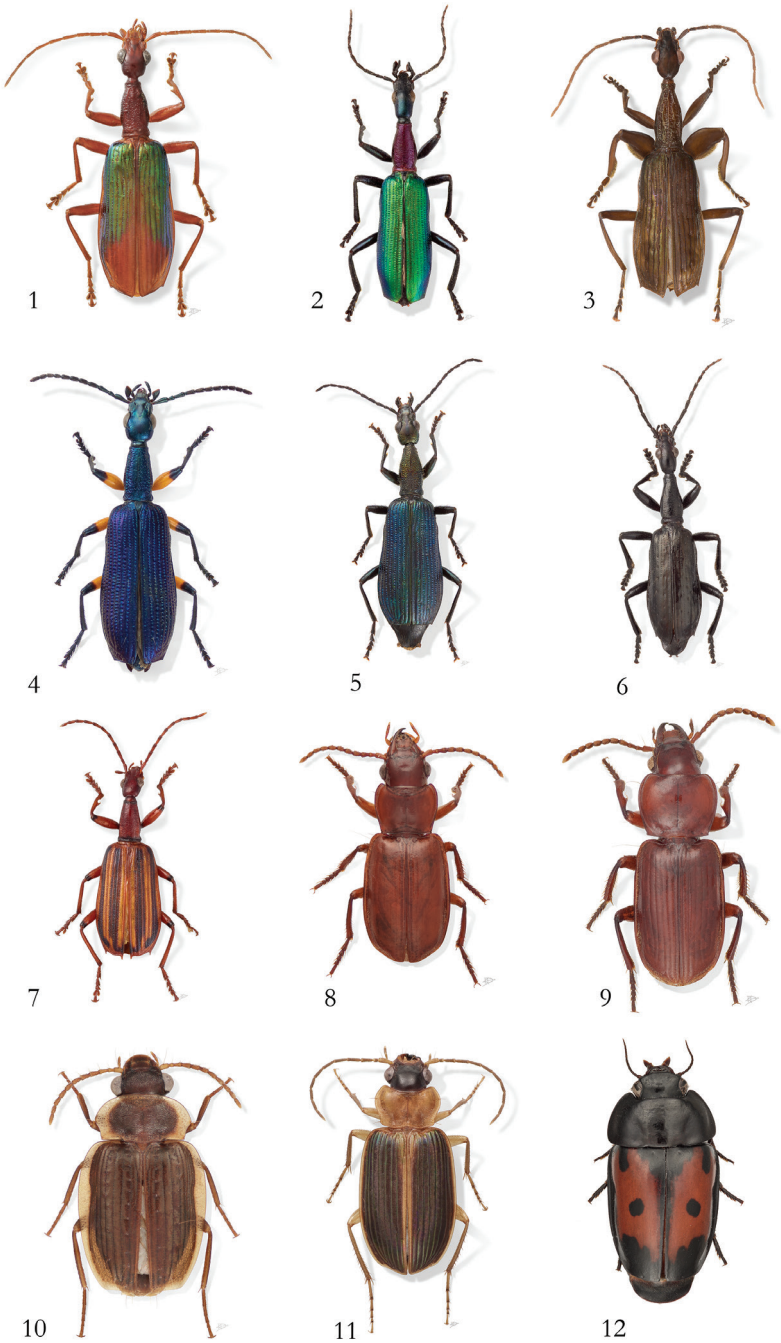

Figure 1–12. Photos of species described by Terry Erwin. **1** *Agra katewinsletae* Erwin, 2002 **2** *A. vation* Erwin, 1983 **3** *A. schwarzeneggeri* Erwin, 2002 **4** *A. grace* Erwin, 2010 **5** *A. risseri* Erwin, 2010 **6** *A. liv* Erwin, 2002 **7** *A. vate* Erwin, 1986 **8** *Mizotrechus bellorum* Erwin, 2011 **9** *M. edithpiafae* Erwin, 2011 **10** *Hybopteroides karolynae* Erwin & Ball, 2012 **11** *Badister amazonus* Erwin & Ball, 2011 **12** *Guyanemorpha spectabilis* Erwin, 2013. Photos: Karolyn Darrow.

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RESEARCH ARTICLE

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A new genus of Coelotinae (Araneae, Agelenidae) from southern China

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Abstract

One new genus of the spider subfamily Coelotinae, *Flexicoelotes* **gen. n.**, with five new species is described from southern China: *F. huyunensis* **sp. n.** (female), *F. jiaohanyanensis* **sp. n.** (male and female), *F. jinlongyanensis* **sp. n.** (male and female), *F. pingzhaiensis* **sp. n.** (female), *F. xingwangensis* **sp. n.** (male and female).

Keywords

Taxonomy, spider, coelotine, SE Asia, Guanxi, Yunnan

Introduction

Coelotine spiders are common in the northern hemisphere. So far, a total of 646 valid species belonging to 23 genera (Wang 2012, Kim and Ye 2013, Kim and Ye 2014, Seo 2014, Ye and Kim 2014, Chen et al. 2015, Jiang and Chen 2015) are known worldwide, and 19 genera are known in Asia. The genera *Alloclubionoides* Paik, 1992, *Hypocoelotes* Nishikawa, 2009, *Tegecoelotes* Ovtchinnikov, 1999 are distributed in Far East Russia and East Asia. The other 16 genera: *Bifidocoelotes* Wang, 2002, *Coelotes* Blackwall, 1841, *Draconarius* Ovtchinnikov, 1999, *Femoracoelotes* Wang, 2002, *Himalcoelotes* Wang, 2002, *Iwogumoa* Kishida, 1955, *Leptocoelotes,* Wang 2002, *Lineacoelotes* Xu, Li & Wang, 2008, *Longicoelotes* Wang, 2002, *Notiocoelotes* Wang, Xu &

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Li, 2008, *Orumcekia* Koçak & Kemal, 2008, *Pireneitega* Kishida, 1955, *Platocoelotes* Wang, 2002, *Robusticoelotes* Wang, 2002, *Spiricoelotes* Wang, 2002 and *Tonsilla* Wang & Yin, 1992, are distributed in southern China and adjacent regions (Japan, Laos and northern Vietnam).

Wang (2012) revised most of the coelotine spiders based on type material. Twenty-two new coelotine species were reported from China and adjacent regions after 2012. Among them, 6 were found in southern China (Chen et al. 2015, Jiang and Chen 2015), 9 were known from Korea (Kim and Ye 2013, Kim and Ye 2014, Seo 2014, Ye and Kim 2014), and 7 were known from Japan (Koumura 2013).

In this paper, we describe a new genus of Coelotine spiders, *Flexicoelotes* gen. n., and five new species. All species were collected from caves in Guangxi and Yunnan, China.

Materials and methods

Specimens were examined with a Leica M205C stereomicroscope. Images were captured with an Olympus C7070 wide zoom digital camera (7.1 megapixels) mounted on an Olympus SZX12 dissecting microscope. Epigynes and male palps were examined after dissection from the spiders' bodies. The epigyne was cleared by boiling it in a 10% KOH solution before taking photos of the vulva.

All measurements were obtained using a Leica M205C stereomicroscope and are given in millimeters. Leg measurements are given as: Total length (femur, patella + tibia, metatarsus, tarsus). Only structures (palp and legs) of the left side of the body are described and measured. The terminology used in the text and the figure legends follows Wang (2002). Abbreviations used in this paper and in the figure legends are: A = epigynal atrium; ALE = anterior lateral eye; AA = anterior apophysis; AME = anterior median eye; AME-ALE = distance between AME and ALE; AME-AME = distance between AME and AME; ALE-PLE = distance between ALE and PLE; C = conductor; CD = copulatory duct; CDA = dorsal conductor apophysis; CF = cymbial furrow; E = embolus; EB = embolic base; ET = epigynal teeth; FD = fertilization duct; H = epigynal hood; LTA = dorso-retrolateral tibial apophysis; MA = median apophysis; PA = patellar apophysis; PLE = posterior lateral eye; PME = posterior median eye; PME-PLE = distance between PME and PLE; PME-PME = distance between PME and PME; RTA = retrolateral tibial apophysis; S = spermatheca; SH = spermathecal head; SST = spermathecal stalk; ST = subtegulum; T = tegulum.

A partial fragment of the mitochondrial gene cytochrome oxidase subunit I (COI) was amplified and sequenced for *F. huyunensis* sp. n., *F. jiaohanyanensis* sp. n., *F. jinlongyanensis* sp. n., *F. pingzhaiensis* sp. n., and *F. xingwangensis* sp. n. following the protocol in Miller et al. (2009). Primers used in this study are: LCO1490 (5'-CWACAAAYCATARRGATATTGG-3') (Folmer et al. 1994) and HCO2198zz (5'-TAAACTTCCAGGTGACCAAAAAATCA-3') (this study). All sequences were blasted in GenBank. The accession numbers are provided in Table 1.

Table 1. Voucher specimen information.

Species	GenBank accession number	Sequence length	Collection localities
Flexicoelotes huyunensis sp. n.	KT727020	1194 bp	TanjiawanVillage, Malipo County, Wenshan Prefecture, Yunnan Province, China
Flexicoelotes jiaohanyanensis sp. n.	KT727021	1194 bp	Equan Village, Jingxi County, Baise City, Guangxi Zhuang Autonomous Region, China
Flexicoelotes jinlongyanensis sp. n.	KT727018	1194 bp	Yongning Village, Napo County, Baise City, Guangxi Zhuang Autonomous Region, China
Flexicoelotes pingzhaiensis sp. n.	KT727019	1194 bp	Pingzhai Village, Xichou County, Wenshan Prefecture, Yunnan Province, China
Flexicoelotes xingwangensis sp. n.	KT727017	1194 bp	Xingwang Village, Debao County, Baise City, Guangxi Zhuang Autonomous Region, China

All of the specimens (including molecular vouchers) are deposited in the Institute of Zoology, Chinese Academy of Sciences (IZCAS) in Beijing, China.

Systematics

Family Agelenidae C.L. Koch, 1837
Subfamily Coelotinae F.O.P.-Cambridge, 1893

Genus *Flexicoelotes* gen. n.
http://zoobank.org/3F8CE486-FF6F-40B1-926B-9F605AC5A40D

Type species. *Flexicoelotes jiaohanyanensis* sp. n.

Etymology. The generic name is derived from the species' similarity to *Coelotes* and the Latin adjective "flexus", meaning "bent, curved", referring to the shape of the conductor. The gender is masculine.

Diagnosis. Males can be easily distinguished from other coelotines, except *Tonsilla* Wang & Yin, 1992 and *Lineacoelotes* Xu, Li & Wang, 2008, by the broad conductor, the spoon-like median apophysis, and the elongate cymbial furrow. They can be distinguished from *Tonsilla* by the bent conductor apex, rather than a lobed conductor, the presence of an anterior apophysis, and the broad cymbial furrow (Fig. 2A–C; Wang and Yin 1992: figs 3–5). They can be distinguished from *Lineacoelotes* by the broad, bent and less modified conductor, the presence of an anterior apophysis, and the thin, simple patellar apophysis (Fig. 2A–C; Xu et al. 2008: figs 13–15). Females can be easily distinguished from other coelotines, except *Tonsilla* and *Lineacoelotes*, by the long epigynal teeth and the absence of epigynal hoods. They can be distinguished from *Tonsilla* by the large and simple atrium, rather than a posteriorly extended anterior atrial margin, an atrium with the anterior part wider than the posterior part, epigynal teeth that are separated rather than near one another, the short and posteriorly located

spermathecae, and the broad, long copulatory ducts (Fig. 3A–B; Wang and Yin 1992: figs 8–10). They can be distinguished from *Lineacoelotes* by the large atrium, the short, simple spermathecae, and the absence of a long, coiled spermathecal head (Fig. 3A–B; Xu et al. 2008: figs 11–12).

Description. *Flexicoelotes* are small to medium-sized, with a total length of 4–9 mm; chelicerae with three promarginal and two retromarginal teeth; male palp with one patellar apophysis; RTA with pointed tip, extending beyond the distal margin of the tibia; LTA short; conductor broad and wider than tibia; median apophysis spoon-like; anterior apophysis present; epigynal teeth very long; atrium large; spermathecae simple, located posteriorly; copulatory ducts broad, located dorsal to the spermathecae.

Distribution. China (Yunnan, Guangxi) (Fig. 9).

Flexicoelotes huyunensis **Chen & Li, sp. n.**
http://zoobank.org/56FD85EE-4EA5-4740-B0ED-5BD6F4E92C26
Figs 1, 9

Type material. Holotype ♀: China: Yunnan Province: Wenshan Prefecture: Malipo County, Tanjiawan Village, Huyun Cave, N23°21'36", E105°02'03", elevation: 1464 m, 8.VIII.2010, Z.Y. Yao, X.X. Wang and C.X. Wu leg.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female can be distinguished from *F. jiaohanyanensis* sp. n. by the short epigynal teeth (1/2 of atrial height, whereas they are almost subequal to atrial height in related species) and the broad, short and opaque copulatory ducts (Fig. 1A–B).

Description. Female (holotype): Total length 6.01. Carapace 3.20 long, 2.17 wide. Abdomen 2.81 long, 1.80 wide. Eye sizes and interdistances: AME 0.09, ALE 0.17, PME 0.11, PLE 0.15; AME-AME 0.05, AME-ALE 0.03, PME-PME 0.08, PME-PLE 0.08. Leg measurements: I: 11.73 (3.09, 4.00, 2.80 1.84); II: 10.89 (2.94, 3.60, 2.66, 1.69); III: 10.04 (2.72, 3.20, 2.64, 1.48); IV: 12.90 (3.40, 4.05, 3.65, 1.80). Epigyne: atrium large, occupying 2/3 of epigynal plate; teeth long, located in atrial anterior margin, about 1/2 of atrial height and separated by their length; hoods absent; spermathecae simple, located in posterior part of epigyne; copulatory ducts broad, occupying 3/4 of epigynal plate, covering most of the spermathecae (Fig. 1A–B).

Distribution. Known only from the type locality (Fig. 9).

Flexicoelotes jiaohanyanensis **Chen & Li, sp. n.**
http://zoobank.org/707B61A7-12F8-4008-AC62-7DF270525FDF
Figs 2–3, 9

Type material. Holotype ♂: China: Guangxi Zhuang Autonomous Region: Baise City: Jingxi County, Equan Village, Jiaohanyan Cave, N23°06'22", E106°24'02", elevation: 697 m, 23.XII.2012, Z.G. Chen and Z. Zhao leg. **Paratypes:** 3♀3♂, same data as holotype.

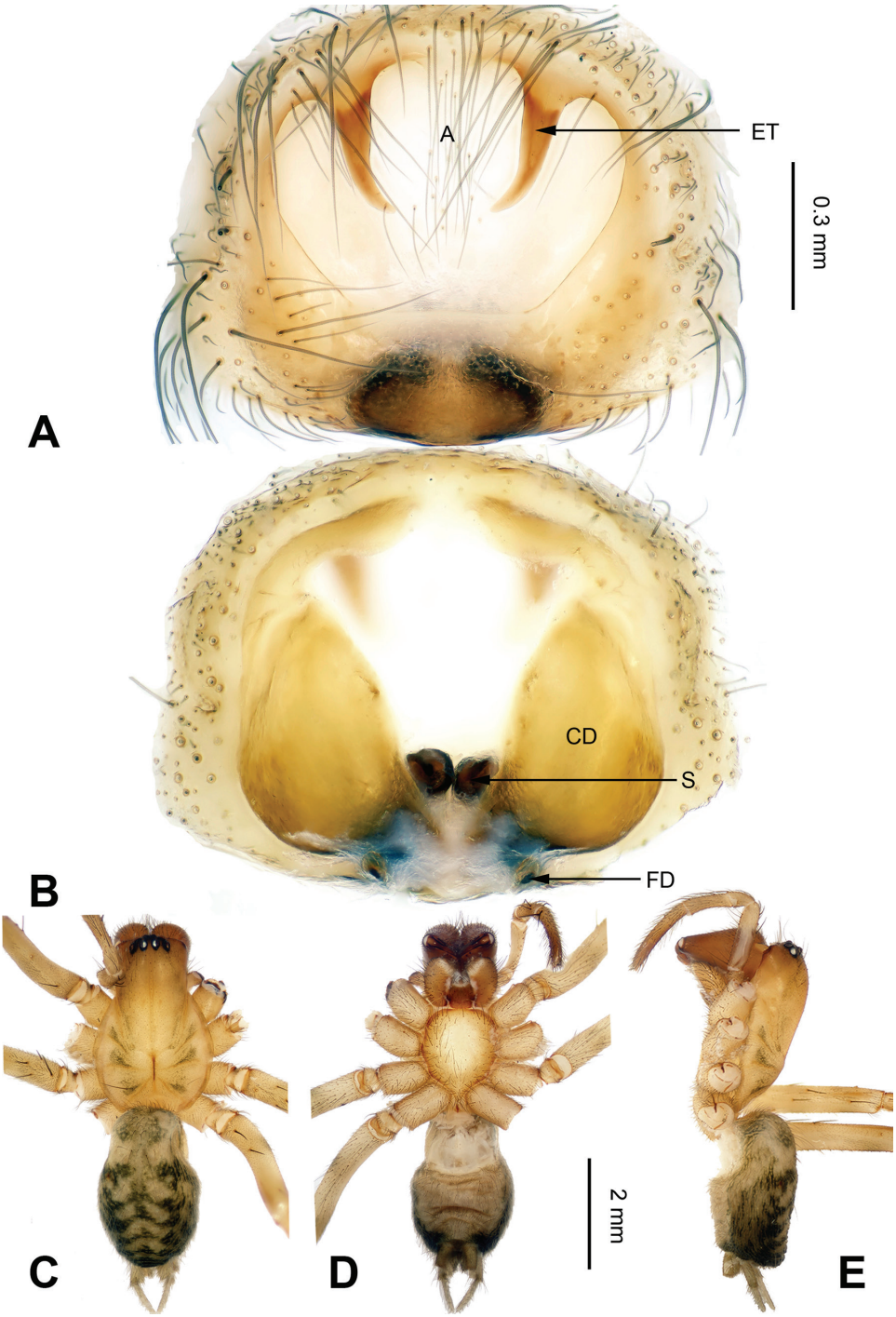

Figure 1. *Flexicoelotes huyunensis* sp. n., holotype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Female habitus, dorsal view **D** Female habitus, ventral view **E** Female habitus, lateral view. Scale bars: equal for **A**, **B**; equal for **C, D, E**.

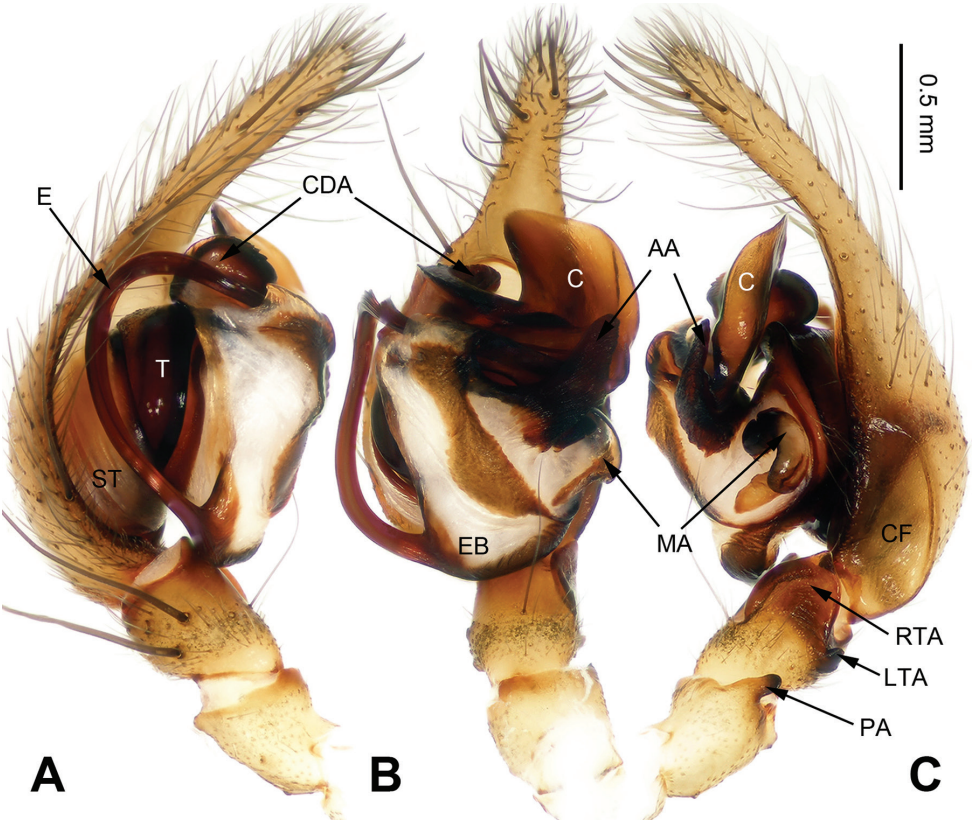

Figure 2. *Flexicoelotes jiaohanyanensis* sp. n., holotype male. **A** Left palp, prolateral view **B** Left palp, ventral view **C** Left palp, retrolateral view. Scale bar: equal for **A, B, C**.

Etymology. The specific name is derived from the type locality; adjective.

Diagnosis. The male can be easily distinguished from other coelotines by the broad, dark conductor and the broad anterior apophysis (Fig. 2A–C). The female can be easily distinguished from other coelotines by the large atrium, occupying more than 1/2 of the epigynal plate, the very long epigynal teeth that are subequal to the height of the atrium, and the translucent copulatory ducts (Fig. 3A–B).

Description. Male (holotype): Total length 6.58. Carapace 3.88 long, 2.70 wide. Abdomen 3.24 long, 2.15 wide. Eye sizes and interdistances: AME 0.13, ALE 0.18, PME 0.17, P LE 0.18; AME-AME 0.04, AME-ALE 0.03, PME-PME 0.08, PME-PLE 0.07. Leg measurements: I: 15.16 (3.85, 5.10, 3.91, 2.30); II: 14.07 (3.72, 4.35, 3.76, 2.24); III: 13.13 (3.64, 3.95, 3.63, 1.91); IV: 17.05 (4.00, 5.26, 5.45, 2.34). Palp: patellar apophysis long, subequal to half of patellar width; RTA with pointed tip, extending beyond distal margin of tibia; LTA short, approximately less than 1/5 length of RTA; cymbial furrow short, about 1/4 length of cymbium; conductor broad, apex bent, with blunt tip; dorsal conductor apophysis small; median apophysis small, spoon-like; anterior apophysis broad, with blunt tip; embolus filiform, beginning at 6:30 to 7 o'clock position (Fig. 2A–C).

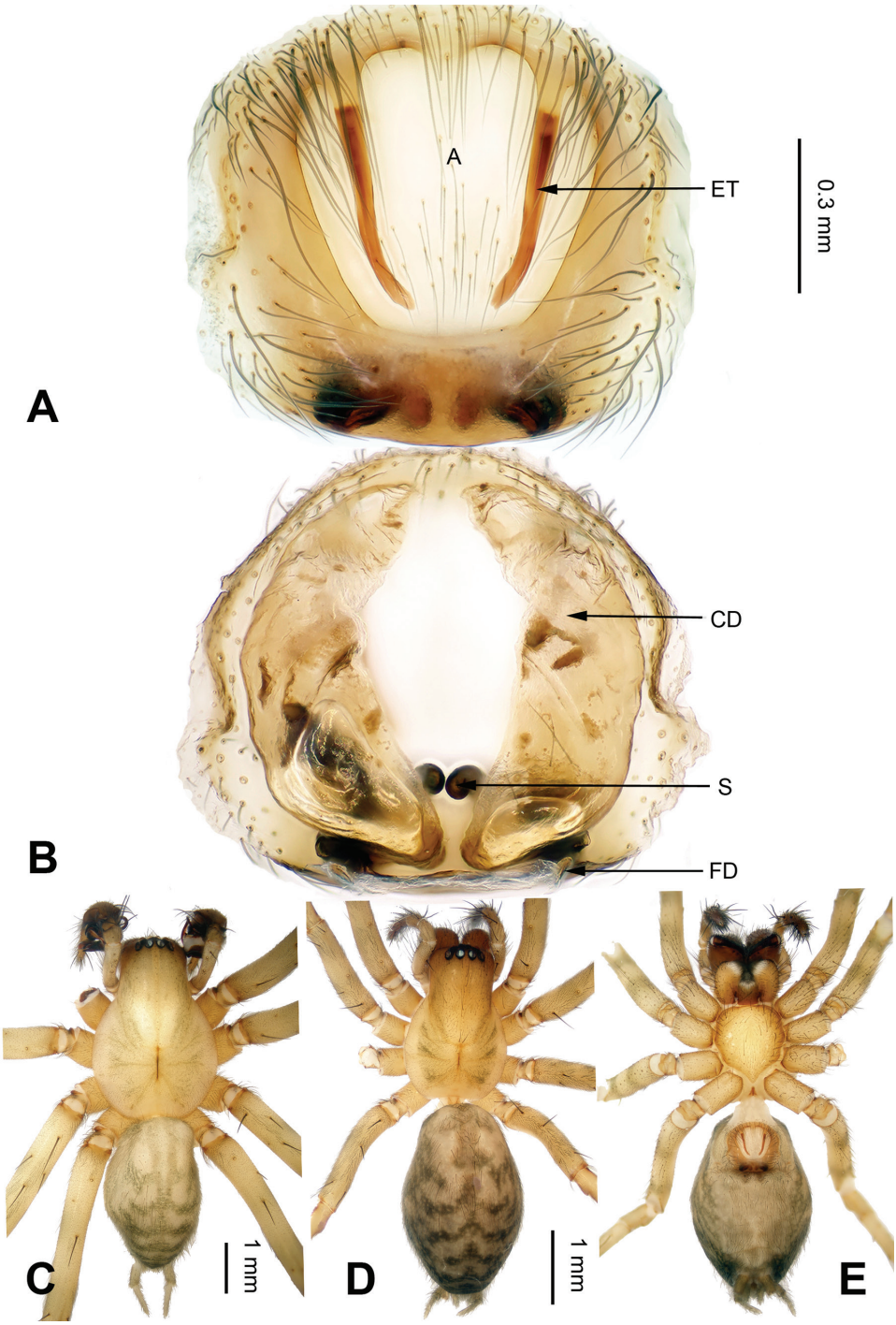

Figure 3. *Flexicoelotes jiaohanyanensis* sp. n., one of paratype females. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Male habitus, dorsal view **D** Female habitus, dorsal view **E** Female habitus, ventral view. Scale bars: equal for **A, B**; equal for **D, E**.

Female (one of paratypes): Total length 4.76. Carapace 2.84 long, 1.92 wide. Abdomen 3.56 long, 2.16 wide. Eye sizes and interdistances: AME 0.11, ALE 0.18, PME 0.13, PLE 0.17; AME-AME 0.02, AME-ALE 0.03, PME-PME 0.07, PME-PLE 0.06. Leg measurements: I: 10.54 (2.88, 3.60, 2.48, 1.58); II: 9.35 (2.60, 3.12, 2.31, 1.32); III: 8.84 (2.44, 2.75, 2.43, 1.22); IV: 11.50 (3.00, 3.60, 3.36, 1.54). Epigyne: atrium large, occupying 2/3 of epigynal plate; teeth located in anterior atrial margin, separated from each other, very long, and subequal to the height of the atrium; hoods absent; spermathecae simple, located in posterior part of epigyne, covered mostly by the copulatory ducts in dorsal view; copulatory ducts broad, occupying 2/3 of epigynal plate (Fig. 3A–B).

Distribution. Known only from the type locality (Fig. 9).

Flexicoelotes jinlongyanensis **Chen & Li, sp. n.**
http://zoobank.org/ADC405C1-E049-4132-8274-5FCCC8D3930A
Figs 4–5, 9

Type material. Holotype ♂: China: Guangxi Zhuang Autonomous Region: Baise City: Napo County, Yongning Village, Jinlongyan Cave, N23°21'16", E105°51'01", elevation: 826 m, 22.XII.2012, Z.G. Chen and Z. Zhao leg. **Paratypes:** 2♀3♂, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The male can be distinguished from *F. jiaohanyanensis* sp. n. by the large dorsal conductor apophysis, the short, thin anterior apophysis, the short patellar apophysis, the complex and light-colored conductor, and the long, broad cymbial furrow (Fig. 4A–C). The female can be distinguished from *F. jiaohanyanensis* sp. n. and *F. huyunensis* sp. n. by the narrow posterior part of atrium and the unique shape of the copulatory ducts (Fig. 5A–B).

Description. Male (holotype): Total length 6.85. Carapace 3.55 long, 2.55 wide. Abdomen 3.30 long, 2.05 wide. Eye sizes and interdistances: AME 0.13, ALE 0.17, PME 0.17, PLE 0.19; AME-AME 0.06, AME-ALE 0.02, PME-PME 0.06, PME-PLE 0.07. Leg measurements: I: 14.35 (3.80, 4.70, 3.65, 2.20); II: 13.22 (3.52, 4.20, 3.35, 2.15); III: 12.29 (3.25, 3.68, 3.52, 1.84); IV: 16.20 (4.15, 4.85, 4.90, 2.30). Palp: patellar apophysis short; RTA with pointed tip, extending slightly beyond distal margin of tibia; LTA short, about 1/5 length of RTA; cymbial furrow long, about 1/2 length of cymbium; conductor broad, with bent apex; dorsal conductor apophysis large; median apophysis small, spoon-like; anterior apophysis short, apex is thinner than basal part; embolus filiform, beginning at 6 o'clock position (Fig. 4A–C).

Female (one of paratypes): Total length 8.15. Carapace 3.55 long, 2.50 wide. Abdomen 4.60 long, 2.95 wide. Eye sizes and interdistances: AME 0.13, ALE 0.18, PME 0.18, PLE 0.17; AME-AME 0.09, AME-ALE 0.04, PME-PME 0.10, PME-PLE 0.11. Leg measurements: I: 12.44 (3.27, 4.23, 2.95, 1.99); II: 11.16 (3.08, 3.64, 2.68, 1.76); III: 10.48 (2.88, 3.28, 2.76, 1.56); IV: 13.38 (3.68, 4.25, 3.75, 1.70). Epigyne: atrium large, occupying 1/2 of epigynal plate; teeth long, located in atrial anterior

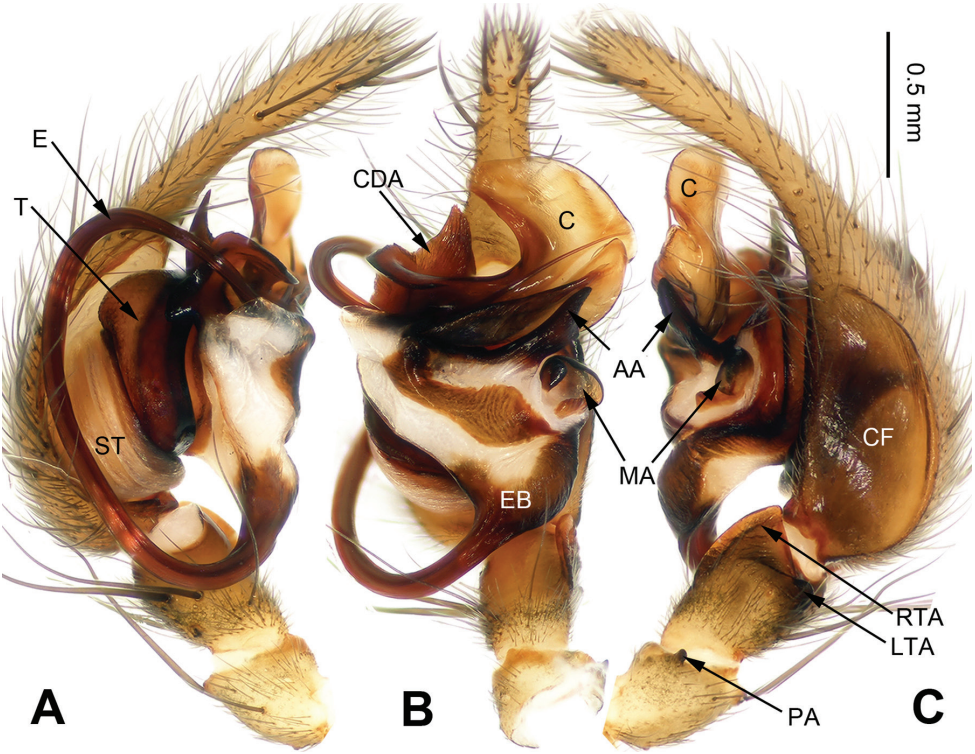

Figure 4. *Flexicoelotes jinlongyanensis* sp. n., holotype male. **A** Left palp, prolateral view **B** Left palp, ventral view **C** Left palp, retrolateral view. Scale bar: equal for **A, B, C**.

margin, about 3/4 of atrial height; hoods absent; spermathecae simple, located posteriorly, covered mostly by copulatory ducts; copulatory ducts broad, occupying 3/4 of epigynal plate (Fig. 5A–B).

Distribution. Known only from the type locality (Fig. 9).

Flexicoelotes pingzhaiensis **Chen & Li, sp. n.**
http://zoobank.org/F23B1DEF-BF52-497C-B2D4-54344E36B20D
Figs 6, 9

Type material. Holotype ♀: China: Yunnan Province: Wenshan Prefecture: Xichou County, Pingzhai Village, Wuming Cave, N23°23'04", E104°46'28", elevation: 1405 m, 5.VIII.2010, Z.Y. Yao, X.X. Wang and C.X. Wu. leg. **Paratypes:** 2♀, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The female can be distinguished from *F. jiaohanyanensis* sp. n. and *F. huyunensis* sp. n. by the subtriangular shape of the atrium, about 1/5 width of the anterior part, the large, oval copulatory ducts and the long, slender spermathecal stalks,

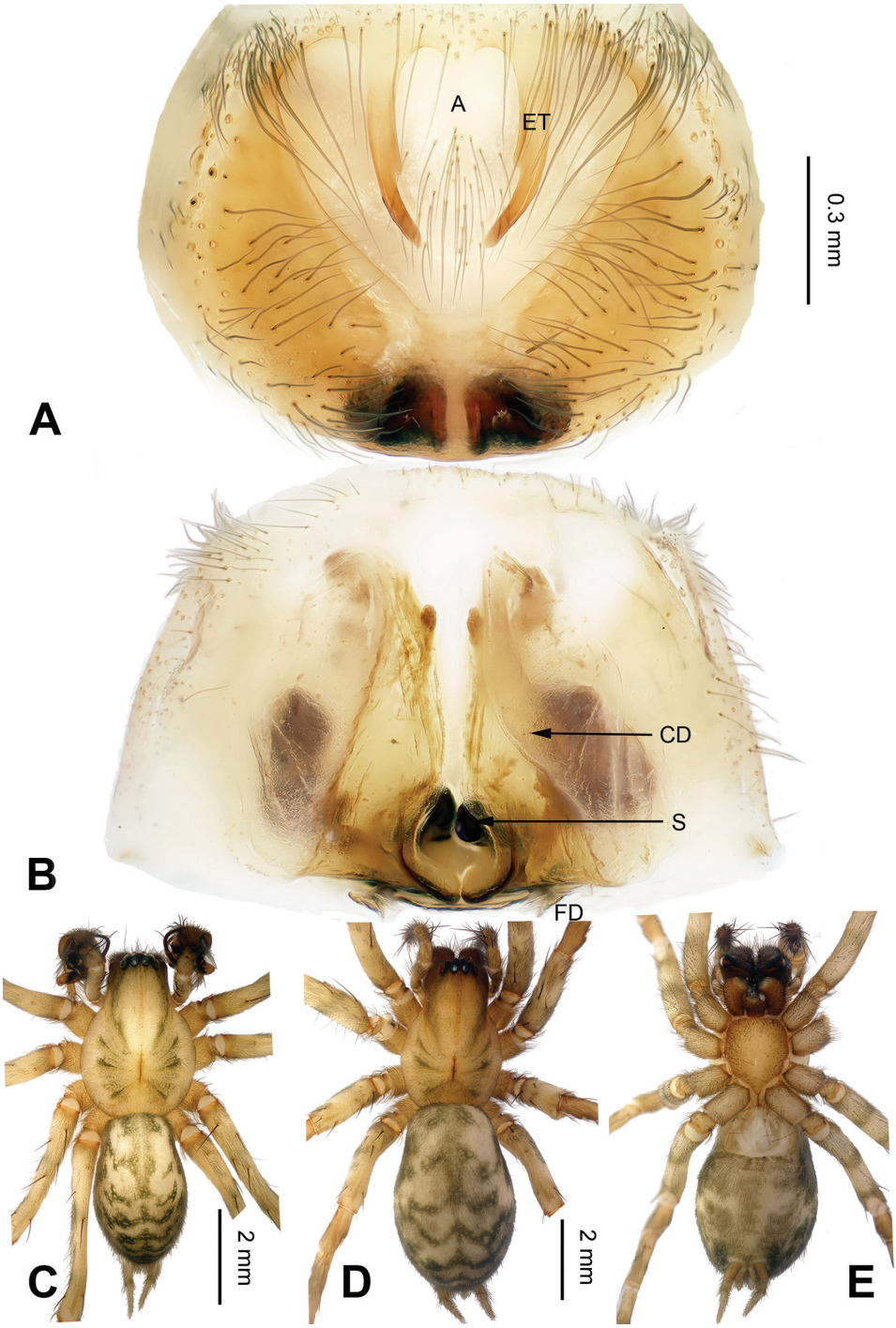

Figure 5. *Flexicoelotes jinlongyanensis* sp. n., one of paratype females. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Male habitus, dorsal view **D** Female habitus, dorsal view **E** Female habitus, ventral view. Scale bars: equal for **A, B**; equal for **D, E**.

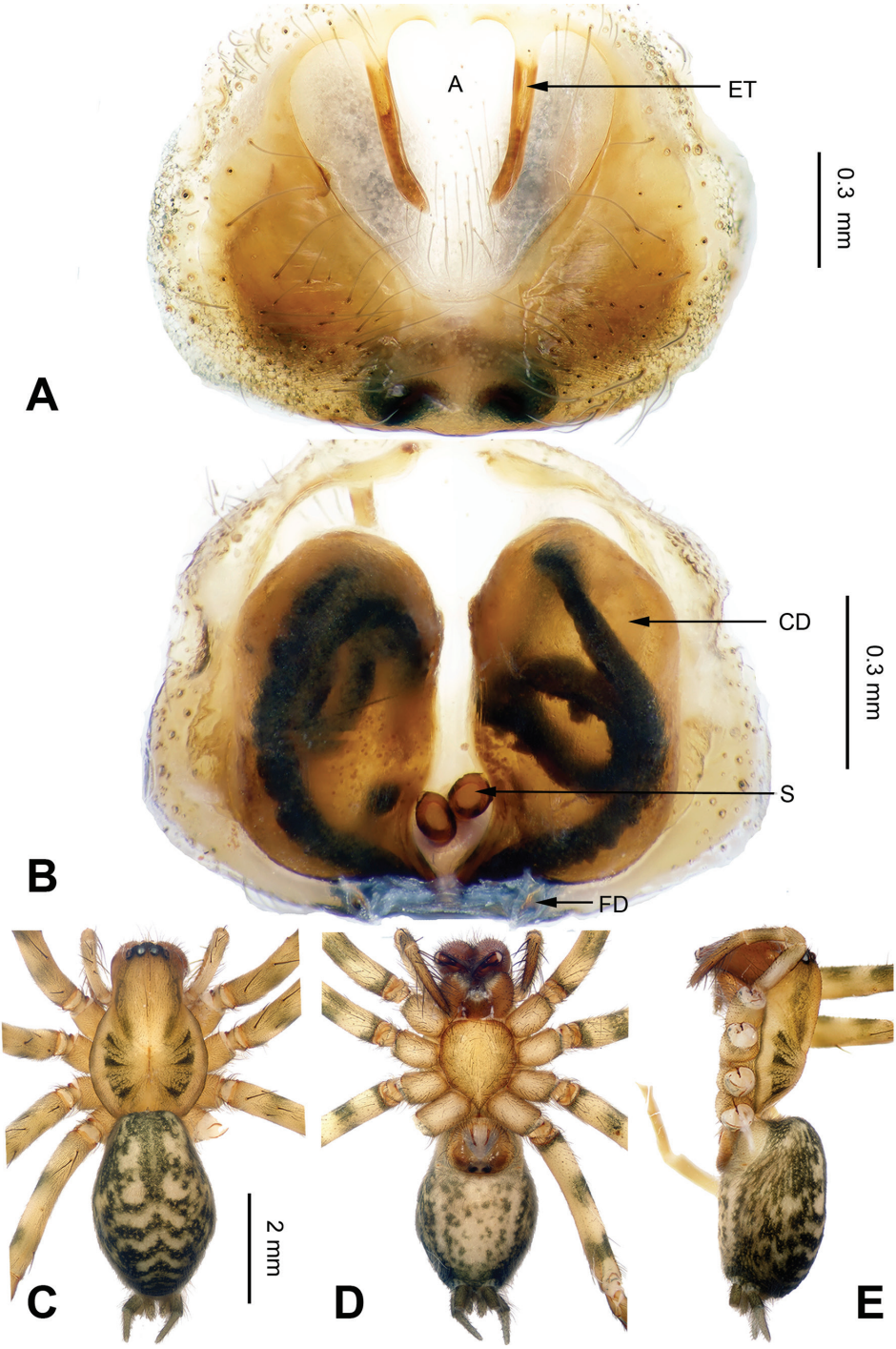

Figure 6. *Flexicoelotes pingzhaiensis* sp. n., holotype female. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Female habitus, dorsal view **D** Female habitus, ventral view **E** Female habitus, lateral view. Scale bars: equal for **C, D, E**.

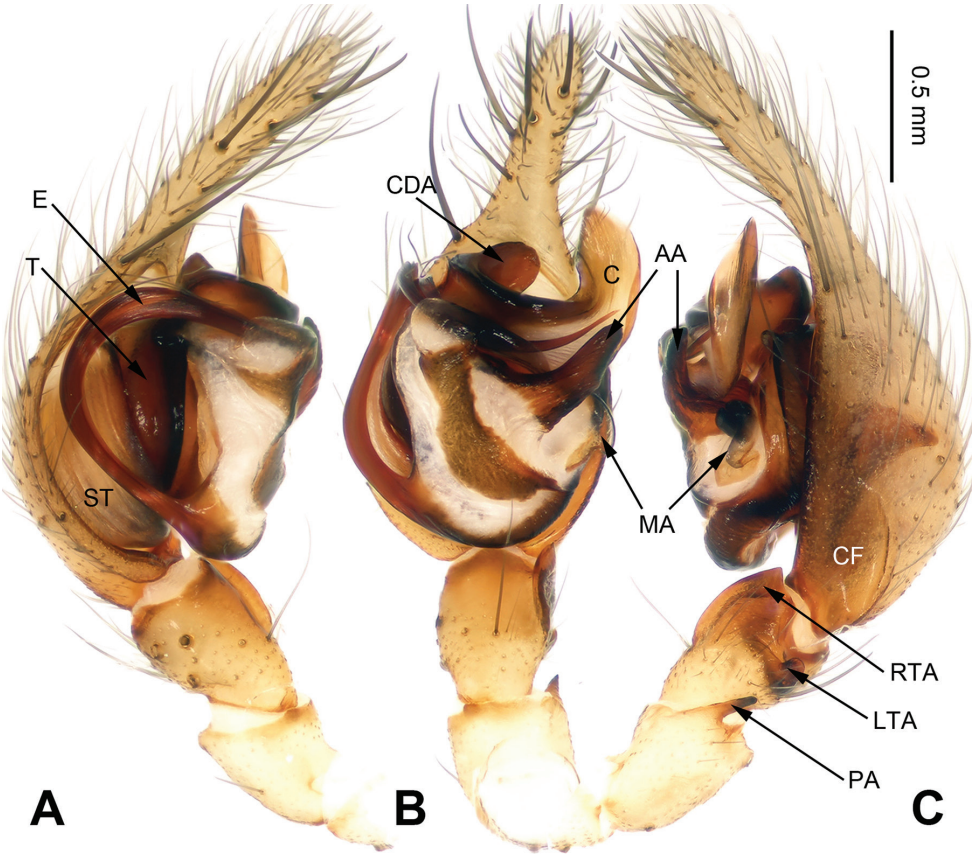

Figure 7. *Flexicoelotes xingwangensis* sp. n., holotype male. **A** Left palp, prolateral view **B** Left palp, ventral view **C** Left palp, retrolateral view. Scale bar: equal for **A, B, C**.

and can be distinguished from *F. jinlongyanensis* sp. n. by the oval copulatory ducts, and the long, slender spermathecal stalks (Fig. 6A–B).

Description. Female (holotype): Total length 6.52. Carapace 3.16 long, 2.22 wide. Abdomen 3.36 long, 2.25 wide. Eye sizes and interdistances: AME 0.12, ALE 0.17, PME 0.16, PLE 0.17; AME-AME 0.07, AME-ALE 0.02, PME-PME 0.08, PME-PLE 0.07. Leg measurements: I: 11.16 (3.04, 3.76, 2.60 1.76); II: 10.04 (2.84, 3.20, 2.44, 1.56); III: 9.23 (2.56, 2.92, 2.40, 1.35); IV: 12.12 (3.32, 3.80, 3.40, 1.60). Epigyne: atrium large, occupying 2/3 of epigynal plate; teeth long, located in atrial anterior margin, about 2/3 of atrial height; hoods absent; spermathecae simple, located in posterior of epigyne, covered mostly by copulatory ducts; spermathecal stalks long, slender, and convoluted; copulatory ducts broad, occupying 4/5 of epigynal plate (Fig. 6A–B).

Distribution. Known only from the type locality (Fig. 9).

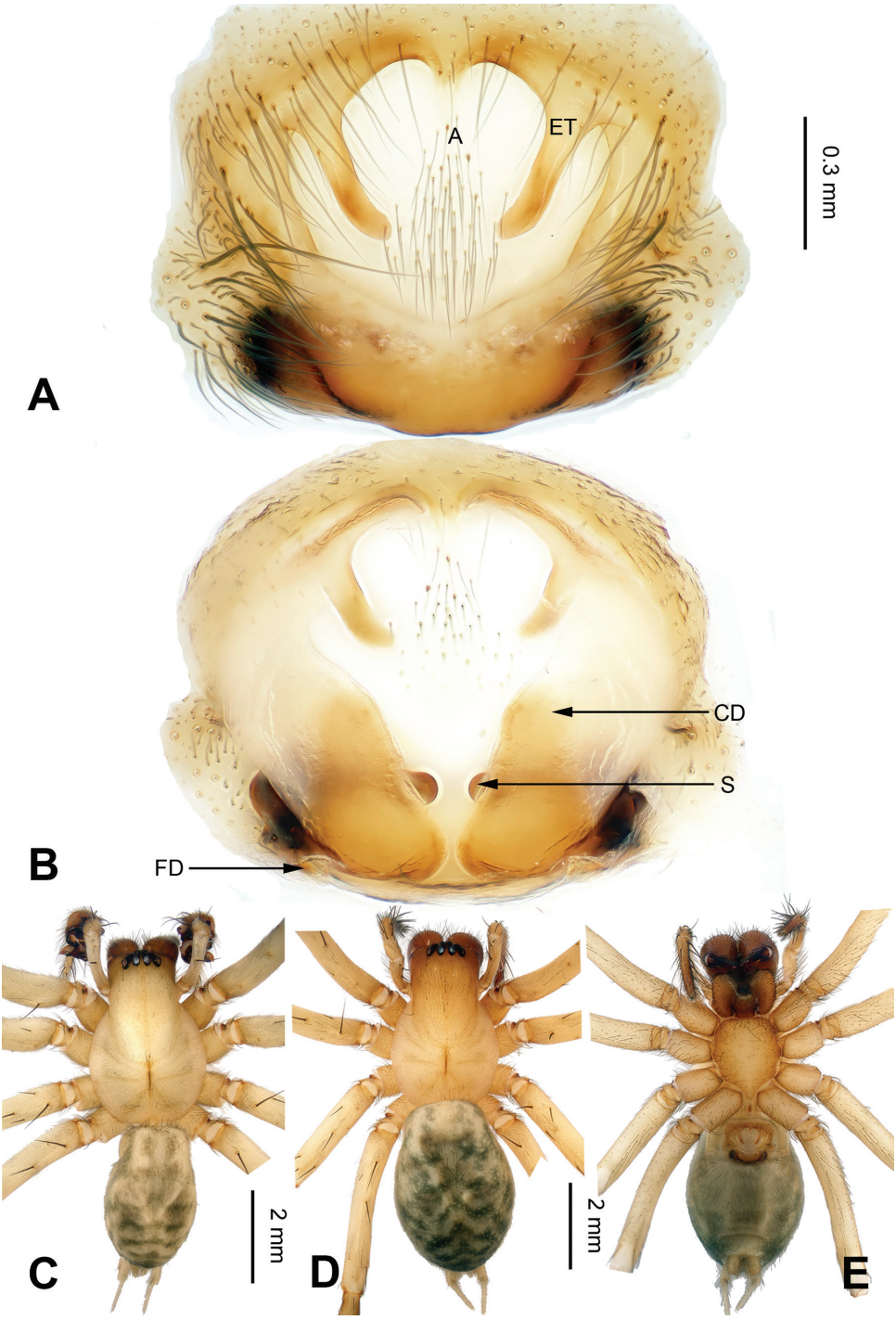

Figure 8. *Flexicoelotes xingwangensis* sp. n., one of paratype females. **A** Epigyne, ventral view **B** Vulva, dorsal view **C** Male habitus, dorsal view **D** Female habitus, dorsal view **E** Female habitus, ventral view. Scale bars: equal for **A, B**; equal for **D, E**.

Flexicoelotes xingwangensis **Chen & Li, sp. n.**
http://zoobank.org/B2D49C18-8651-4491-85C9-94AEB55D879B
Figs 7–9

Type material. Holotype ♂: China: Guangxi Zhuang Autonomous Region: Baise City: Debao County, Xingwang Village, Wuming Cave, N23°14'16", E106°38'35", elevation: 632 m, 19.XII.2012, Z.G. Chen and Z. Zhao. leg. **Paratypes:** 3♀2♂, same data as holotype.

Etymology. The specific name refers to the type locality; adjective.

Diagnosis. The male can be distinguished from *F. jiaohanyanensis* sp. n. and *F. jinlongyanensis* sp. n. by the longer and more slender patellar apophysis, the thin conductor, the large, oval dorsal conductor apophysis in ventral view, and the short cymbial furrow (Fig. 7A–C). The female can be distinguished from *F. jiaohanyanensis* sp. n., *F. huyunensis* sp. n., *F. jinlongyanensis* sp. n., and *F. pingzhaiensis* sp. n. by the small and nearly hexagonal atrium, the short and light-colored epigynal teeth, and the widely separated fertilization ducts (Fig. 8A–B).

Description. Male (holotype): Total length 6.80. Carapace 3.72 long, 2.52 wide. Abdomen 3.08 long, 1.96 wide. Eye sizes and interdistances: AME 0.13, ALE 0.20, PME 0.15, PLE 0.17; AME-AME 0.05, AME-ALE 0.02, PME-PME 0.06, PME-PLE 0.09. Leg measurements: I: 16.01 (4.29, 5.19, 3.97, 2.56); II: 14.56 (3.85, 4.68, 3.78,

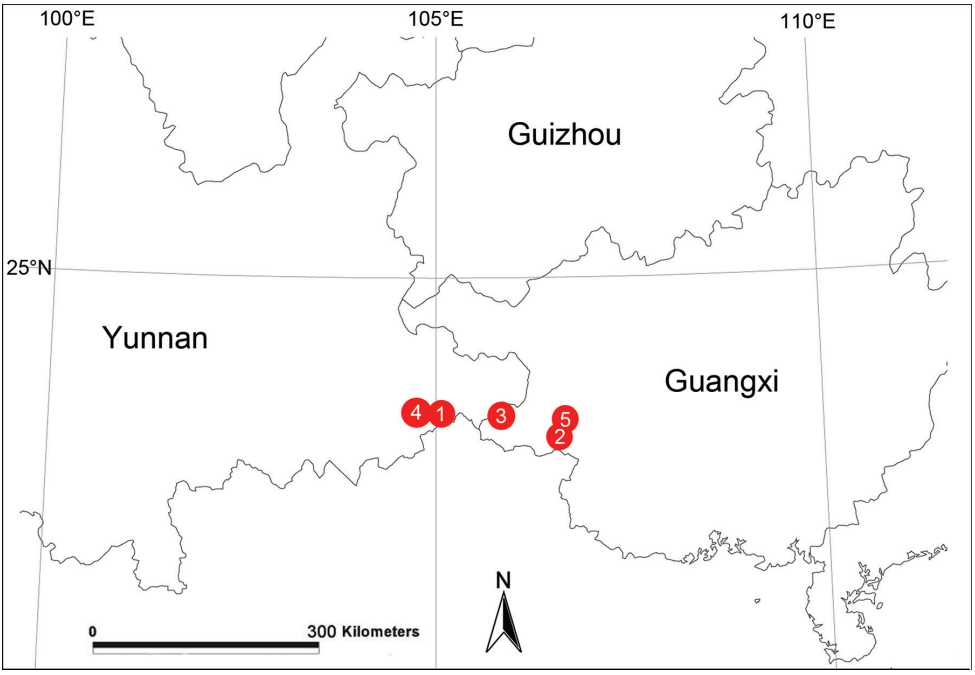

Figure 9. Localities of new *Flexicoelotes* species from China. **1** *F. huyunensis* sp. n. **2** *F. jiaohanyanensis* sp. n. **3** *F. jinlongyanensis* sp. n. **4** *F. pingzhaiensis* sp. n. **5** *F. xingwangensis* sp. n.

2.25); III: 13.50 (3.60, 4.05, 3.90, 1.95); IV: 17.57 (4.50, 5.26, 5.45, 2.36). Palp: patellar apophysis long, subequal to patellar width; RTA with pointed tip, extending beyond distal margin of tibia; LTA long, about 1/3 length of RTA; cymbial furrow short, about 1/5 length of cymbium; conductor broad, with bent apex; dorsal conductor apophysis large; median apophysis small, spoon-like; anterior apophysis broad, with blunt tip; embolus filiform, beginning at 7:30 o'clock position (Fig. 7A–C).

Female (one of paratypes): Total length 7.64. Carapace 3.64 long, 2.53 wide. Abdomen 4.00 long, 2.78 wide. Eye sizes and interdistances: AME 0.13, ALE 0.20, PME 0.15, anterior apophysis PLE 0.17; AME-AME 0.06, AME-ALE 0.04, PME-PME 0.10, PME-PLE 0.11. Leg measurements: I: 13.48 (3.65, 4.60, 3.25, 1.98); II: 12.31 (3.40, 4.05, 3.05, 1.81); III: 11.40 (3.24, 3.60, 3.08, 1.48); IV: 15.46 (4.05, 4.75, 4.88, 1.78). Epigyne: atrium large, occupying 2/3 of epigynal plate; teeth long, located in atrial anterior margin, about 2/3 of atrial height; hoods absent; spermathecae simple, located posteriorly; copulatory ducts broad, occupying 2/3 of epigynal plate, covering most of spermathecae (Fig. 8A–B).

Distribution. Known only from the type locality (Fig. 9).

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RESEARCH ARTICLE

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A remarkable new genus and a new species of chewing louse (Phthiraptera, Ischnocera, Philopteridae) from Brazil

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Abstract

A new genus of chewing louse as *Bobdalgleishia*, and its type species *Bobdalgleishia stephanophallus* **sp. n.** (Phthiraptera) belonging to the *Brueelia*-complex (Ischnocera: Philopteridae) are described. Adults of the new species are fully described, illustrated and compared morphologically with the type species of *Motmotnirmus* Mey & Barker, 2014, which is its closest relative. The type host of *B. stephanophallus* is a subspecies of the great jacamar *Jacamerops aureus ridgwayi* Todd, 1943, an endemic Amazonian bird distributed in northern Brazil, and the type locality is the State of Pará. *Bobdalgleishia* is a remarkable genus with unique morphological and chaetotaxic characters which readily separate it from other members of the *Brueelia*-complex, in particular by having the first two marginal temporal and ocular setae very long.

Keywords

Brueelia-complex, *Bobdalgleishia*, Jacamar, Galbulidae, Ischnocera, new genus, new species, Neotropical

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Introduction

The known chewing lice of the family Philopteridae (Ischnocera) parasitic on Galbuliformes (Aves) are six species of the genus *Mayriphilopterus* Mey, 2004 (*Philopterus*-complex) (Mey 2004, Valim and Linardi 2007) and eight species of the genus *Picicola* Clay & Meinertzhagen, 1938 (*Degeeriella*-complex) (Oniki and Emerson 1981, Valim and Linardi 2006, Price and Weckstein 2006). In addition, there is an unconfirmed record of the menoponid *Menacanthus caudatus* (Giebel, 1876) (Amblycera, Menoponidae) on *Galbula ruficauda* Cuvier (Galbulidae) (Giebel 1876, Price et al. 2003). However, there is no previous record of chewing lice from the great jacamar, *Jacamerops aureus* (Statius-Müller, 1776) (Price et al. 2003, Price and Weckstein 2006).

Among the genera belonging to the *Brueelia*-complex (Philopteridae *sensu lato*), some have a worldwide distribution, while others are geographically endemic and/or with host distribution restricted to certain host group (Mey and Barker 2014, Valim and Palma 2015). Six named genera of the *Brueelia*-complex contain species endemic to the Neotropical Region: *Bizarrifrons* Eichler, 1938 on Icteridae (Aves: Passeriformes: Passeri); *Formicaphagus* Carriker, 1957 on Thamnophilidae, Conopophagidae and Formicariidae (Aves: Passeriformes: Tyranni); *Formicaricola* Carriker, 1957 on Formicariidae; *Pseudocophorus* Carriker, 1940 on Cotingidae (Aves: Passeriformes: Tyranni); *Motmotnirmus* Mey & Barker, 2014 on Momotidae (Aves: Coraciiformes); and *Paragoniocotes* Cummings, 1916 on Psittacidae (Aves: Psittaciformes). At least four other louse genera, with species parasitic on several groups of avian hosts (e.g. Passeriformes, Trogoniformes, Piciformes), also occur in the Neotropical Region, but are not restricted to that region (Mey and Barker 2014). Our aim is to provide a detailed morphological description of a seventh endemic genus within the *Brueelia*-complex from the neotropics. The new genus is distinct from its sympatric relatives, as well as from all other genera included in the *Brueelia*-complex, both by morphological and chaetotaxic characters in both sexes. This is the first record of a member of the *Brueelia*-complex on Galbuliformes hosts.

Methods

The specimens examined for the descriptions of the new taxa were collected from a bird skin held at the Museu Nacional do Rio de Janeiro (MNRJ), as recommended by Mey (2002). All lice collected were in good conditions and were permanently slide-mounted using Canadian balsam, as described by Palma (1978). They are deposited in the Phthiraptera collection of the Museu de Zoologia da Universidade de São Paulo (MZUSP). The geographic coordinates given for the locality of the skins searched for lice were taken from Paynter and Traylor (1991).

The nomenclature of louse head features and setae follows Clay (1951) and Mey (1994); the occipital head sensilla (*s1–s5*) are named following Valim and Silveira (2014). Abdominal chaetotaxy patterns are described following those in Cicchino and

Castro (1996) and Cicchino and Valim (2008) for members of the *Brueelia*-complex. The classification and nomenclature of hosts follow Dickinson (2003).

Abbreviations used for both body and head setae and sensilla are given in italic and lower case (see Clay 1951, Mey 1994, Valim and Silveira 2014): *ads* = anterior dorsal seta, *as* = anterior seta, *avs* = anterior ventral seta, *dsms* = dorsal submarginal seta, *mds* = mandibular seta, *mts* = marginal temporal seta, *os* = ocular seta, *pas* = preantennal seta, *pcs* = preconal seta, *pns* = postnodal seta, *pos* = preocular seta, *ppss* = prothoracic postspiracular seta, *pts* = postemporal seta, *s* = spine-like seta of pterothorax, *s1–s5* = occipital head sensilla, *tr* = trichoid setae, *vsms* = ventral submarginal seta.

Images were taken using a Leica DFC295 digital camera installed at a Leica DM5000 B optical microscope, and measurements of specimens were taken using the software Leica Application Suite (LAS) v.4.1.0. Measurements are in millimeters, and identified by the following abbreviations: ANW anterior notch width (from tips of marginal carina), PAW preantennal width (at level of *pas*), TW temple width (at level just anterior to *mts1*), HL head length (at midline including the hyaline margin), PW prothorax width (at the widest point), PL prothorax length (at midline), PEW pterothorax width (at the posterior level), PEL pterothorax length (at midline), AWV abdomen width on segment V, AL abdomen length, BAW basal apodeme width (at the widest point), BPW basal plate width, MEW mesosoma width (at the widest point), PRW penial ring width (breadth of gonopore opening), PAW paramere width (at its mid length), BAL basal apodeme length, MEL mesosoma length (including the tip of gonopore), PAL paramere length, BAMEL = BAL+MEL, GL total genitalia length (from proximal tip of basal apodema to distal tip of paramere), TL total body length (from hyaline margin of head to end of tergite XI).

Taxonomic treatment

Phthiraptera Haeckel, 1896
Ischnocera Kellogg, 1896
Philopteridae Burmeister, 1838 (*sensu lato*)

The *Brueelia*-complex

Currently, this complex comprises 17 named genus-group taxa. A full account of the morphology and discussions on the genera included in this complex can be found in Mey and Barker (2014) and in Valim and Palma (2015).

***Bobdalgleishia* Valim & Cicchino, gen. n.**
http://zoobank.org/2F42B28A-D727-4E6C-8F11-44E882AFFD90

Type species. *Bobdalgleishia stephanophallus* Valim & Cicchino, sp. n.

Diagnosis. *Bobdalgleishia* is morphologically close to *Motmotnirmus* (from Momotidae hosts), being the only members of the *Brueelia*-complex with *mts2* very long (subequal to *mts3*) on the temporal margin, and with sternal segments II–VI lacking sclerotization and with more than one pair of setae. All other genera of this complex have only the *mts3* very long and the sternites usually bear one pair of setae each. However, both sexes of *Bobdalgleishia* can be distinguished from those of *Motmotnirmus*, as well as from those of all other genera of the *Brueelia*-complex, by having *os* and *mts1–3* very long, and postspiracular present on segment II. In both sexes of *Motmotnirmus* only *mts2* and *mts3* are very long, the *os* and *mts1* are very short (see Fig. 3D), and postspiracular seta is absent on tergite II. Furthermore, males are different in the shape of the parameres (triangular and flattened in *Motmotnirmus*), by a tubiform mesosome (short and compact in *Motmotnirmus*, see Fig. 3E), and a gonopore with a distinct crown with indentations (gonopore without crown in *Motmotnirmus*, see Fig. 3E). In females, tergites XI are fused with IX+X (in *Motmotnirmus* they are separated), and each gonaphophysis has only one spine-like seta (Fic. 3C) (a patch of 3–4 thin setae in *Motmotnirmus*, as in Fig. 3F). Females of species of *Paragoniocotes* also have setae on the gonapophyses, but more than one each side, in addition to having *os* and *mts1–2* very short. Lastly, a very long ocular seta (*os*) is also found in one species of *Rostrinirmus* Złotorzycka, 1964 (not recognized as valid by Price et al. 2003, Valim and Palma 2015) but, as in most other members of the *Brueelia*-complex, they have very short *mts1–2*.

Bobdalgleishia is distinct from the type species of *Brueelia sensu stricto* at first glance by (1) the *as2*, *as3* and *dsms* set on the hyaline margin, not on the sclerotised portion of the head; (2) presence of *as3*; (3) *os* and *mts1–2* are macrochaeta. Furthermore, the type species of *Bobdalgleishia* is the only member of the *Brueelia*-complex having, in both sexes, (1) four long setae on the temple margin: *os* and *mts1–3*; (2) *pos* short and set on eye lens; (3) one pair of anterior setae on tergite II; and (4) sterna II–VI with more than one pair of setae and lacking sclerotized plates. In addition, females lack the cross-piece on the vulvar margin, and their tergite XI is fused with IX+X.

Description. Both sexes. *Head*: Antennal scape and flagellomeres not enlarged; preantennal region short and tapered, conspicuously symmetric (Figs 1–2, 3A) and antennae monomorphic; anterior dorsal head plate indicated only by its anterolateral angles, but basically fused on its lateral and posterior portions with the head's roof. Marginal carina medially divided and without lateral interruption; hyaline margin present, reaching only the distal portion of anterior dorsal head plate (ADHP), and set between anterior setae (*as2*) and widely anterior to ADHP. Dorsal setae: *ads* short and set on dorsal sclerotized surface; *dsms* medium-long and arising from preantennal suture which divides the marginal carina with discrete lateral division. Except for *dsms* medium-long, all other anterior setae short. Anterior setae *2* (*as2*) and *as3* present and set on hyaline margin. Ventral anterior head plate indistinct, ventral carina interrupted medially and fused anteriorly on each side with the marginal carina; each half of the ventral carina entirely sclerotized and with flattened lobes to attachment of pulvinus. Ocular setae (*os*) very long, *pos* very short and set more ventrally on ocular lens. Tem-

poral carina not developed and postantennal region without sutures; both postnodal seta (*pns*) and post-temporal seta (*pts*) present and short, but never sensilliform. Head sensilla present (*s1–s5*), each bearing a much reduced seta, and *s5* set closer to *s3–s4* than to *pns*. Presence of *s5* is not regular and bilateral in all studied specimens, it maybe a duplication of *s4*. Marginal temporal setae 1–3 (*mts1–3*) very long, and *mts4–5* very short (Fig. 3A). Occipital carina present, weakly sclerotized. Gular plate roughly rhombic in shape and well sclerotized (Figs 1–2, 3A).

Thorax: As in Figs 1–2. Prothorax roughly rectangular, with rounded lateral sides and posterior margin nearly straight, with one pair of long prothoracic postspiracular setae (*ppss*). Pterothorax without signs of division between meso- and metathorax, with one ventral spine-like, and one dorsal trichoid, and circa of seven setae on each side of its posterior margin. Legs without distinctive features, except for the thickened dorsal incrassation of the legs II and III, thicker on femurs and with irregular inner border.

Abdomen: Similar in both sexes (Figs 1–2); tergite II (actually I+II) with one long pair of anterior setae (reminiscent of those from tergite I); postspiracular setae present on II–VII; without accessory to postspiracular seta; pleural setae present on IV–VIII; and sutural and innermost setae present each side on tergites II–VII. Sternites II–VI with more than two pairs of setae each. Porotaxy: sensilla present on tergites II–V.

Male. Antennal scape and flageromeres not enlarged, as in females. Subgenital plate faintly delimited and with two pairs of setae at level of sternite VII. Tergal plates IX+X fused, distinct and medially divided, tergite XI indistinct or non-sclerotized. Genitalia as in Fig. 3B, see detailed description below.

Female. Subgenital plate smooth (Fig. 3C), lacking any sclerotization on distal vulvar margin (the "cross piece" of Ansari 1956), posterior end nearly rectangular; with three pairs of setae at level of sternite VII. Tergites XI fused with IX+X, forming a single IX–XI last segment (Figs 2B, 3C).

Etymology. Named in honor to the late and personal friend Robert [Bob] C. Dalgleish (1940–2009) for his special disposition to listen and learn from those who disagree with him on taxonomic issues. Bob was an example of how a taxonomist might make a huge contribution in a relatively short period of time, less than ten years in his second life period of "lousying" with us (his first was during 1966–1972). It is a noun in the singular genitive, masculine.

Bobdalgleishia stephanophallus **Valim & Cicchino, sp. n.**

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Figs 1–2, 3A–C

Type host. *Jacamerops aureus ridgwayi* Todd, 1943 – great jacamar [ridgwayi] (Galbulidae).

Type locality. Alto Rio Cururu, Pará, Brazil.

Diagnosis. *Bobdalgleishia stephanophallus* can be easily separated from the four species of the genus *Motmotnirmus* (*M. marginellus* (Nitzsch [in Giebel], 1866) the type species; *M. xilitla* (Carriker, 1954); *M. guatemalensis* (Dalgleish, 1971), and

Figure 1. *Bobdalgleishia stephanophallus*, habitus in dorsal view: **A** male **B** female. Abbreviations: *mts*, marginal temporal setae 1 and 2; *os*, ocular seta.

M. humphreyi (Oniki and Emerson, 1982)) by the generic characters discussed above, i.e. head chaetotaxy (compare Figs 3A and 3D), male genitalia (compare Figs 3B and 3E), and female gonapophysis (compare Figs 3C and 3F). In addition, tergites VII–VIII in species of *Motmotnirmus* have more than four posterior tergal setae on each segment (Fig. 3F), in *B. stephanophallus* these same segments have fewer setae (males sometimes with 1+1 on VII only) (Fig. 3C).

Description. Male. Habitus as in Figs 1A and 2A. Body pigmentation light-yellow, except for the head marginal carina and pre-antennal nodi strongly brownish (Fig. 1A).

Head as in Figs 1A, 2A and 3A, slightly shorter than wide, with cephalic index (HL/TW) 0.9. Coni well developed and subequal in length with scape. Preantennal

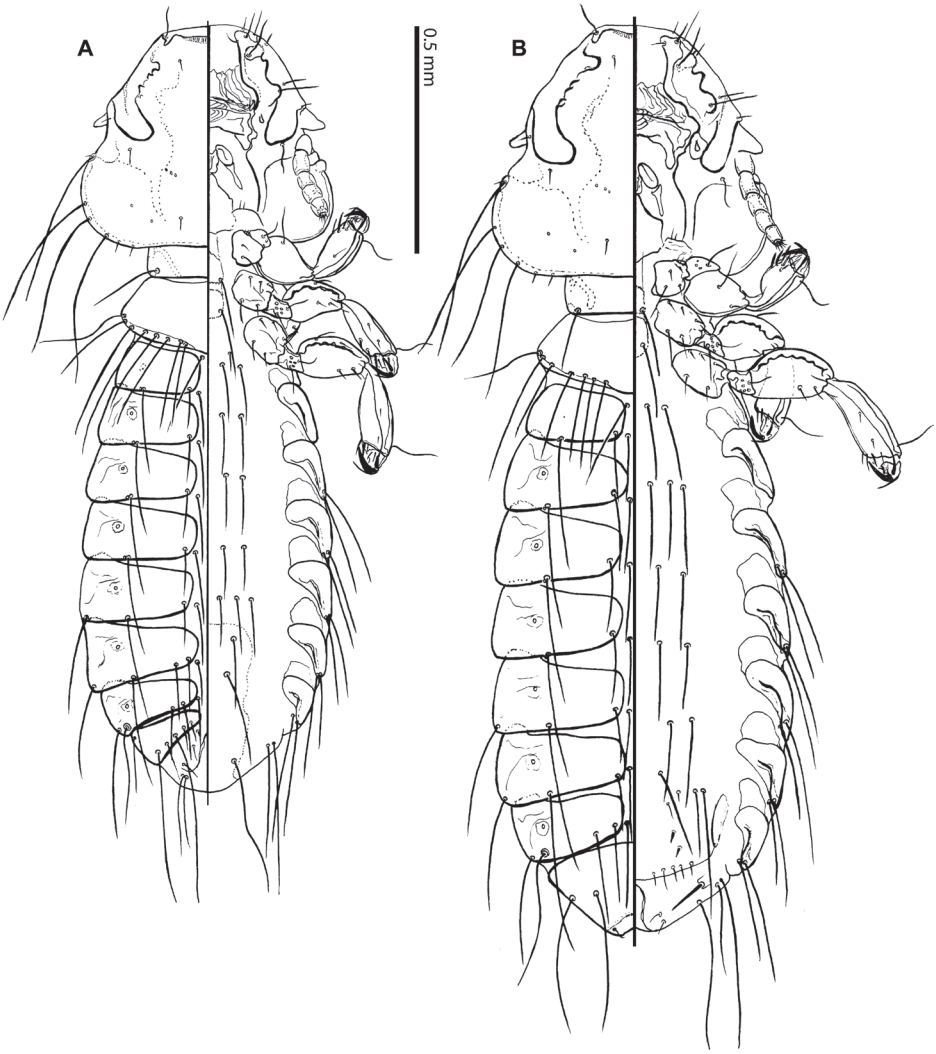

Figure 2. *Bobdalgleishia stephanophallus*, habitus in dorsal-ventral views: **A** male **B** female.

region tapered, preantennal margins slightly convex, and marginal temporal margins rounded. Small and nearly convex hyaline margin between tips of the pre-marginal carina each side (Fig. 3A). Preantennal region with internal margins of carinae distinctly thick and irregular (Figs 1A and 3A). Frontoclypeal suture light and distinct, its nodal area (preantennal nodus) roughly circular in shape and very well sclerotized. Gular plate roughly rhomboid and uniformly pigmented. Temples rounded; marginal temporal carina darker pigmented and medium thick, with its inner margin nearly uniform up to the level of *mts4* (Fig. 3A).

Thorax as in Figs 1A and 2A. Pterothorax with 7 marginal setae on each side (rarely 6 in one or both sides); pterothoracic apodeme (metepisternum) not well pigmented,

reaching the lateral margins of the segment. Meso- and metasternal plates not fused, both grossly rounded and bearing a pair of long setae each.

Abdomen as in Figs 1A and 2A. Tergites uniformly pigmented, except for a small area around spiracles (Fig. 1A). Tergal chaetotaxy: postspiracular long on II–VII; accessory setae absent; and one medium long sutural seta on II–VII. Tergite VIII: trichoid lateral setae thin and medium long, and five setae subequal in length to trichoid setae. Tergite IX+X medially divided, with 2 medium long and 3–4 short setae. Paratergal chaetotaxy: II–III 0; IV–V 2; VI–VIII 3. Paratergites II–VIII with internal incrassation forming an inverted-L on each side of the abdominal segments. Sterna II–VI lacking sclerotized plates, each with four long setae (rarely 2 setae on II, or 6 on VI) set on the soft tegument, one unpaired small and anterior setae on segment II in the holotype. Subgenital plate present and sclerotized, the only sternite visible, but outline completely indistinct (Fig. 2A).

Genitalia as in Fig. 3B. Basal plate proximally wide, narrowing distally, with enlarged thickened lateral margins; parameres allantoid ("sausage-shaped"), their bases without defined head, but completely articulated with basal plate, each bearing one subapical sensillum and one apical microseta; mesosomal complex tube-shape, with 2 ventral pairs of sensilla each side, and distally reaching the mid-length of parameres; gonopore is also a large tube, but narrower than the mesosomal tube, and with a distinct crown bordered with indentations, more conspicuous ventrally (Fig. 3A).

Measurements (n = 2): ANW 0.10; PAW 0.39–0.40; TW 0.51–0.53; HL 0.45–0.47; PW 0.24–0.25; PL 0.13–0.14; PEW 0.35–0.36; PEL 0.13–0.15; AWV 0.51–0.54; AL 0.98–1.07; BAW 0.07–0.09; BPW 0.05–0.07; MEW 0.05; PRW 0.02–0.03; PAW 0.02; BAL 0.16; MEL 0.08–0.09; PAL 0.11–0.12; BAMEL 0.24–0.25; GL 0.26–0.28; TL 1.64–1.70.

Female. Habitus and coloration similar to males (Figs 1B and 2B), except for size and details of terminal segments. Head short, with cephalic index (HL/TW) 0.8. Abdominal tergites II–VII and sternites II–VI as in male for coloration, incrassation, and chaetotaxy.

Pterothorax with 6+5 (11 in total) marginal setae on each side. Tergites II–VIII divided medially, with internal end nearly rounded. Paratergal chaetotaxy: II–III 0; IV–V 2; VI–VIII 3. Sternal plates as in males (Fig. 2B); number of sternal setae on II 5, III 8, IV 4, V 4, VI 5. Tergite VIII: each side with one thin trichoid lateral seta, one innermost seta and one sutural seta (Fig. 3C). Tergites XI fused with those of IX+X (Figs 1B, 2B, and 3C). Morphology and chaetotaxy of terminalia as in Fig. 3C.

Subgenital plate indistinct in the single female studied, with 2–3 small setae on each side (Fig. 3C). Gonapophyses bear one spine-like setae each, both directed medio-posteriorly and arising from a distinct tubercle. Vulva with only two submarginal short spiniform setae on each side, and 10 medium-long thin setae on its posterior margin (Fig. 3C). Area of the subgenital plate with one pair of long medial seta, plus two pairs of medium long setae each side, all along sternum VIII (Fig. 3C).

Measurements (n = 1): ANW 0.10; PAW 0.45; TW 0.59; HL 0.50; PW 0.27; PL 0.15; PEW 0.40; PEL 0.15; AWV 0.62; AL 1.26; TL 1.94.

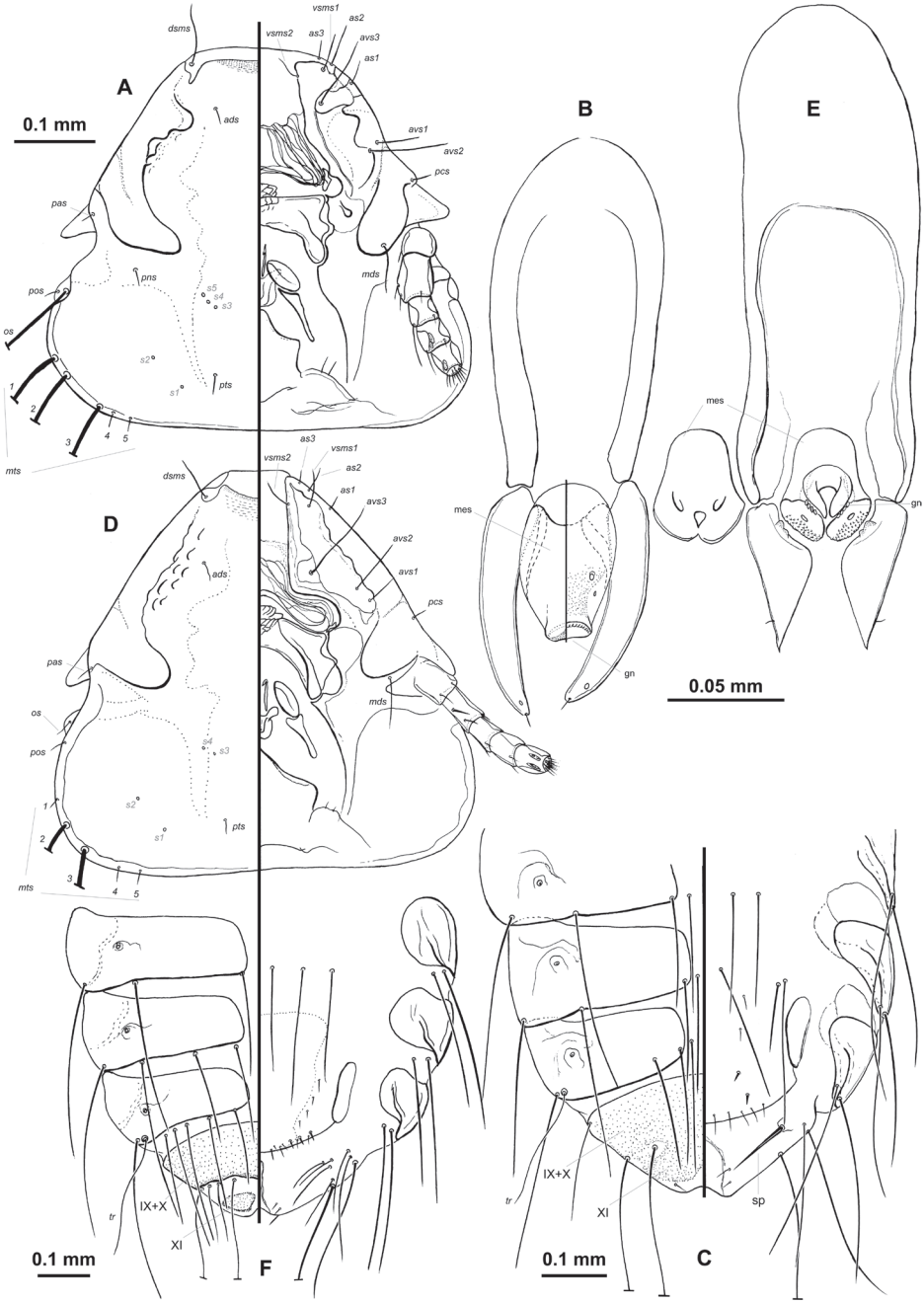

Figure 3. *Bobdalgleishia stephanophallus*: **A** male head in dorso-vental views **B** male genitalia, mesosome in dorso-ventral views **C** female terminalia (VI–XI), in dorso-ventral views. *Motmotnirmus marginellus* **D** male head in dorso-ventral views **E** male genitalia, mesosome in ventral view, detail of mesosomal plate in dorsal view **F** female terminalia (VI–XI), in dorso-ventral views. Abbreviations: gn, gonopore; mes, mesosome; sp, spine-like seta of the gonapophyses; IX, X, XI, last three female abdominal tergites (9th to 11th) [for other abbreviations, see methods].

Etymology. The species epithet is a composite of the Greek words *Στέφανο* (*stephano-*) and *φαλλός* (*-phallus*), which mean 'a crown' and 'the penis'. It makes allusion to the crowned structure on the opening of the male gonopore. It is an adjective in the nominative singular.

Type material. Holotype ♂ (MZUSP #6363), ex *Jacamerops aureus ridgwayi* Todd, 1943 (#A.2880, voucher at MNRJ); BRAZIL: Pará, Alto Rio Cururu (07°12'S, 58°04'W; 50m), 6.VI.1957, H. Sick coll. **Paratypes**: 1♂, 1♀ (MZUSP #6363–6364), same data as holotype.

Additional material examined. *Motmotnirmus marginellus* (Nitzsch [in Giebel], 1866): 3♂, 3♀ (MZUSP #6342–6348), ex *Momotus momota* (Linnaeus, 1766) (Aves: Coraciiformes: Momotidae) (voucher at MZUSP #98878), BRAZIL: Pará, Fazenda Fartura (09°38'04.1"S, 50°28'37.6"W, 160m), Santana do Araguaia, .VIII.2014, A. Gouvea coll.

Remarks. The morphological differences between the single species of *Bobdalgleishia* and those of *Motmotnirmus* are congruent with the evolutionary history of their host groups: Galbuliformes and Coraciiformes, respectively (e.g. Livezey and Zusi 2007, Hackett et al. 2008, Yuri et al. 2013). However, it is surprising to find that the shape of the mesosomal plate and the "crowned" gonopore in the male genitalia of *B. stephanophallus* are unique features among all the species of the *Brueelia*-complex. Some unrelated genera of Philopteridae – *Rallicola* (*Apterricola*) Harrison, 1915 (*Rallicola*-complex) as an example – have mesosomes with similar shape (see Clay 1972: figs 13–15), whereas the mesosome and crowned gonopore are similar to those of some members of the family Heptapsogasteridae – *Rhopaloceras almeidai* Guimarães, 1946: fig 5, as an example. We believe these similarities are the result of evolutionary convergence, and have no phylogenetic implications.

Considering that the Piciformes are also included in the same large group as Galbuliformes and Coraciiformes (e.g., Livezey and Zusi 2007, Hackett et al. 2008, Yuri et al. 2013), this new genus needs to be compared with lice of the *Brueelia*-complex found on those hosts. Species from both Picidae (see Dalgleish 1971) and Ramphastidae (see Cicchino 1983) only have the *mts3* very long (against *os*, *mts1-3* very long in *Bobdalgleishia*). In addition, species from woodpeckers belong to *Brueelia* Kéler, 1936 (*sensu stricto*), whereas those found on toucans to the genus *Traihoriella* Ansari, 1947 (D.R. Gustafsson pers. comm. 2015).

Discussion

Although museum skins are good source of bird ectoparasites (Mey 2002), there are many examples in the literature of louse species described from the wrong hosts, which have taken great time and efforts by later taxonomists to disclose their true host-parasite relationship (e.g. Palma 1994). Although MPV examined approximate-

ly 15 skins of the great jacamar in the MNRJ and a further 21 in MZUSP, the type series of *B. stephanophallus* was found by chance on just one skin collected by H. Sick. Notwithstanding the small number of lice found and the risks involved in describing new louse taxa from museum skins, we accept the record as the result of correct and natural host-louse association. These are our reasons that justify the description of the two new taxa from lice collected on a museum skin, accepting the great jacamar as the true host: (1) more than one pair of specimens were collected, all of the same species, including two males showing that their differential characters were not due to distortion or individual variation; (2) all morphological and phylogenetic relevant characters needed for a complete description are in perfect condition and perfectly visible in all specimens (see Fig. 1); (3) the number and degree of morphological differences between our new taxa and their closest relatives already described in the literature are significant enough to be worthy of publication and dissemination; (4) the male genitalia of *B. stephanophallus* are unique among species of the *Brueelia*-complex; (5) considering that species of *Brueelia sensu lato* have been recorded from several host orders (e.g. Passeriformes, Trogoniformes, Piciformes, Coraciiformes), finding the first member of the *Brueelia*-complex on a species of Galbuliformes is not unexpected; (6) if by any chance, the great jacamar is shown not to be the true, natural host of *B. stephanophallus*, our morphological description is detailed enough for this taxon to be unequivocally recognized on any other host and from any part of globe; (7) the morphological characters we used to describe the new genus *Bobdalgleishia*, will distinguish it from any genus within the family Philopteridae, regardless which host may be its correct, natural host; (8) the morphological features shared between species of *Bobdalgleishia* and *Motmotnirmus* make sense, considering that the Galbuliformes arose from the same related branch which the Coraciiformes (plus Piciformes and Trogoniformes) belong to (Livezey and Zusi 2007, Hackett et al. 2008, Yuri et al. 2013), these being three orders from which species of the *Brueelia*-complex have been recorded.

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RESEARCH ARTICLE

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Revision of the genus *Ficiana* Ghauri and its relationship to other genera in Empoascini (Hemiptera, Cicadellidae, Typhlocybinae)

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Abstract

The empoascine genus *Ficiana* Ghauri is reviewed based on specimens from China. One new *Ficiana* species, *Ficiana aurantia* **sp. n.** is described from Guangxi in south China. An identification key to all species in this genus is provided. The morphological characters of *Ficiana* and related genera in this tribe are discussed.

Keywords

Auchenorrhyncha, Cicadelloidea, morphology, distribution, taxonomy

Introduction

The empoascine genus *Ficiana* was established by Ghauri (1963) based on specimens from Coimbatore (south India) (type species: *Ficiana pruthii* Ghauri, 1963). It is a small genus in Empoascini and easily identified by having a median sulcus on frons, vein CuA of hind wing unbranched, ventral pygofer appendage absent, and subgenital plates fused (Ghauri 1963). This genus is confined to the Oriental region and only one species (the type species) has been reported so far.

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The generic characters of *Ficiana* need to be revised because no additional information had been added to this genus after its establishment. In this paper, a more detailed description based on specimens from China is provided. This is the first report of this genus in the Chinese fauna. In addition, a new species of *Ficiana* from Guangxi in south China is described, and the interpretation of morphology resemblance and reconsider the evolutionary relationship of this genus with related genera in the tribe Empoascini is discussed.

Material and methods

The specimens used in this study are deposited in the Entomological Museum, Northwest A&F University, Yangling, Shaanxi, China (NWAFU). Male genitalia dissections were carried out as described by Oman (1949) and Knight (1965). Line diagrams were drawn using Olympus PM-10AD microscope. Photographs were taken with an automontage QImaging Retiga 4000R digital camera (CCD) stereozoom microscope. The body measurements are from apex of vertex to tip of forewing. Terminology follows Zhang (1990) with the following exceptions: wing venation follows Dworakowska (1993), groups of setae on the subgenital plate follow Southern (1982), and leg chaetotaxy follows Rakitov (1998).

Taxonomy

Genus *Ficiana* Ghauri

Ficiana Ghauri, 1963: 472.

Type species. *Ficiana pruthii* Ghauri, 1963, by original designation.

Description. Body robust. Head including eyes broader than maximum width of pronotum in dorsal aspect (Figs 1, 3). Crown short and broad, rounded anteriorly, anterior and posterior margins subparallel, middle length shorter than width between eyes (Figs 1, 3). Coronal suture distinct, extended onto face and terminating at level of antennal bases (Figs 1, 3, 4), transition of vertex to face rounded in profile (Fig. 2). Face broad, lateral frontal sutures convergent towards base (Fig. 4). Ocelli on margin about equidistant between eye and midline (Figs 1, 3, 4). Pronotum large with sinuate transverse depression (Figs 1–3). Scutellum with median depression. Forewing narrow, apical cells occupying nearly one-third of total length, all three apical veins arise from longitudinal m cell, veins RP, MP' confluent for short distance pre-apically, 2nd apical cell with margins almost parallel apically (Fig. 8). Hindwing with CuA unbranched (Fig. 9). Front femur with dorsoapical pair of macrosetae, AM1 enlarged and situated on ventral margin, intercalary row with one large basal setae and eight smaller setae more distal. Hind femur macrosetae 2+1+1, row AV with 11 macrosetae near apex.

Male abdominal apodemes developed, parallel sided (Fig. 7). Pygofer short, terminally bearing rigid microsetae on each side of lobe, ventral appendage absent, dorsal bridge short (Figs 5, 6, 11, 12). Subgenital plates large and fused throughout almost in whole length except apices, A-group setae absent, B-group setae small and rigid, C-group setae sharply terminated, D-group setae not numerous (Figs 5, 6, 10, 18). Paramere short and robust, setae and sensory pits absent (Figs 5, 6, 10, 17). Connective subtrapezoidal, closely related to aedeagus (Figs 14–16). Aedeagal shaft tubular, ventro-basally produced, dorsoatrium developed (Figs 14, 15). Anal tube appendage distinct (Figs 5, 10, 13).

Remarks. The original illustrations of the type species made the male genital diagnosis of this genus hard to understand, especially the configuration of the aedeagus. Based on our additional new findings, it has a median sulcus of frons (Fig. 4); all apical veins in forewing arising from longitudinal m cell, vein CuA in hind wing unbranched (Figs. 8, 9); ventral pygofer appendage absent (Figs 5, 10, 11); subgenital plates large and fused throughout almost in whole length (Fig. 18); and anal tube appendage present (Figs 5, 10, 13). All of these characters ensure the new species fit the definition of *Ficiana* Ghauri (1963) and it is described here.

Ghauri (1963) noted the aedeagus was "with three pairs of elaborate appendages, as shown in the figure". However, the figures provided by Ghauri, 1963 (Figs L, K) made the characters of aedeagus rather confused. After checking the genital characters of the new *Ficiana* species (specimens deposited in NWAFU), and also Fig. L in Ghauri's illustrations, we believe that Fig. K (aedeagus, in lateral view) was positioned upside down. Moreover, the specimens in NWAFU show the aedeagus with only two pairs of processes [one pair near middle of ventro-basal protrusion and another pair at dorso-basal prolongation of dorsoatrium (latero-distally extended to base of anal tube)] (Figs 14, 15). This paper further defines this genus by including more morphological and revised genital characters.

Distribution. China (Guangxi), India.

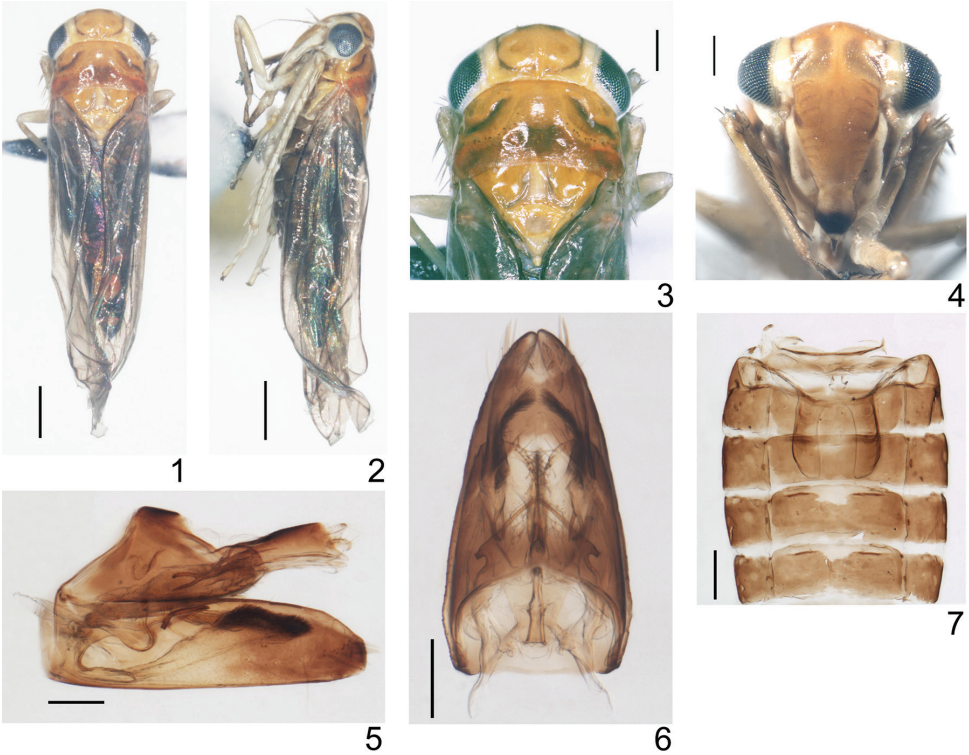
Key to species of the genus *Ficiana* Ghauri (males)

1 Male pygofer triangular, not truncated caudally (Figs 5, 10, 11); anal tube appendage straight, branched apically (Figs 5, 10, 13); paramere spine-like apically, subapex with a short columnar process (Fig. 17) ***F. aurantia* sp. n.**

– Male pygofer nearly hexagonal, truncated caudally (Ghauri, 1963: Fig. 4E); anal tube appendage curved, unbranched apically (Ghauri, 1963: Fig. 4F); paramere not spine-like apically, subapex without columnar process (Ghauri, 1963: Figs 4I, J)..... ***F. pruthii* Ghauri**

***Ficiana aurantia* sp. n.**
http://zoobank.org/E8DC26D0-8EF7-44C7-A227-528A27795F46
Figs 1–18

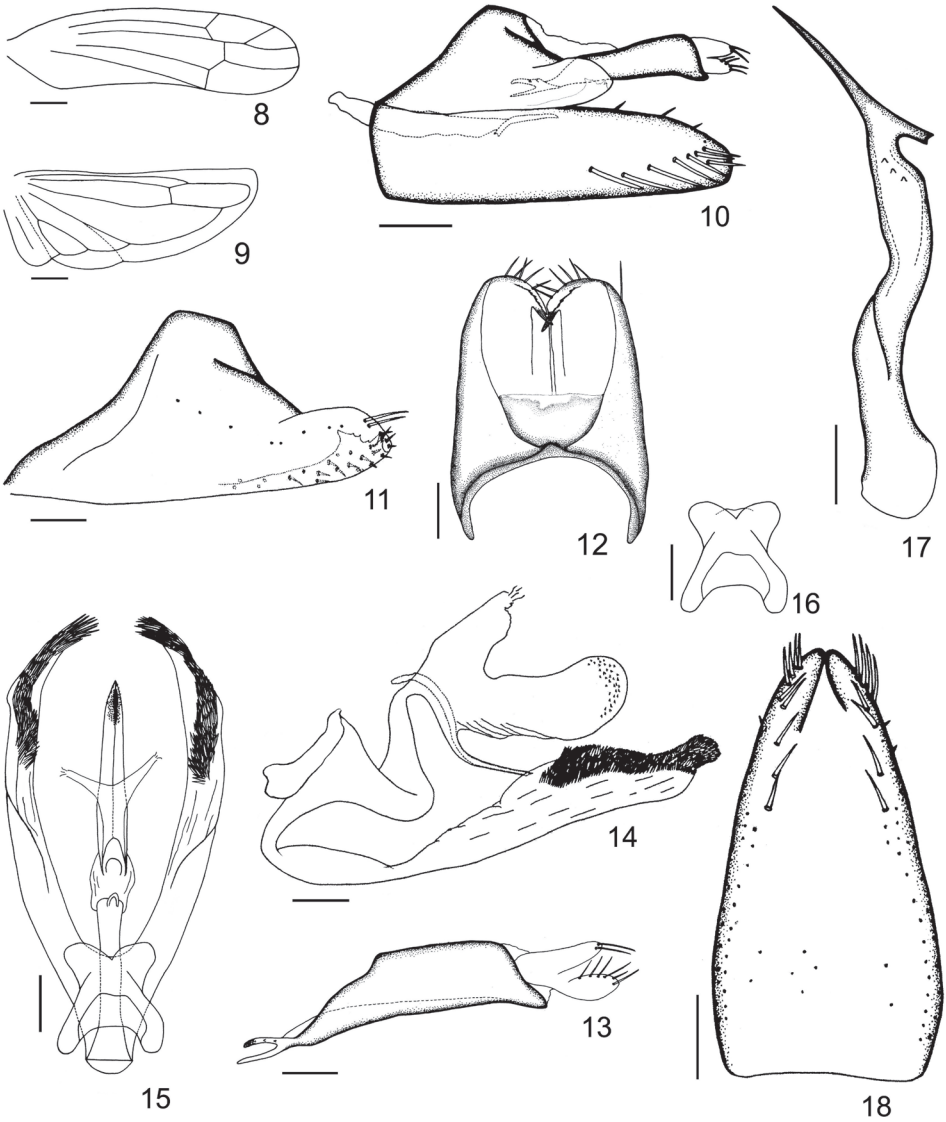
Description. Body length: Male 3.75–4.05 mm.



Figures 1–7. *Ficiana aurantia* sp. n. **1** male adult, dorsal view **2** male adult, left lateral view **3** head and thorax, dorsal view **4** face **5** male genitalia, left lateral view **6** male genitalia, dorsal view **7** abdominal apodemes. Scale bars: 0.5 mm (**1, 2**); 0.2 mm (**3–7**).

Color. General color of male orange. Crown with a brownish shallow depression beside coronal suture, sublaterally near eyes with a narrow blackish stripe on each side which is continuously extended to base of face, the stripes curved near base of vertex (Figs 1, 3, 4). Frontoclypeus with transverse linear stripes laterally, adjacent to the lateral frontoclypeal suture brown with two meniscate, brownish patches, anteclypeus black apically, lorum sordid brownish centrally (Fig. 4). Eyes dark (Figs 1–4). Ocelli circled with whitish creamy patch (Figs 1–4). Pronotum with black, sinuate transverse depression laterally, mid-posteriorly reddish-black, laterobasal angles studded with reddish patches (Figs 1, 3). Centre of scutellum with a quadrate creamy patch anteriorly (Figs 1, 3). Abdomen black (Figs 1, 2). Fore and hindwing subhyaline, vein distinct (Figs 1, 2). Legs greyish (Fig. 2).

Basal abdominal sternal apodemes reaching the end of segment 4 (Fig. 7). Male pygofer almost triangular, distal lobe bearing 2 long and approximately 20 rigid setae, caudo-ventral margin infolded, poorly sclerotized and apically bearing irregular teeth (Figs 5, 10–12); dorsal bridge occupying almost 1/4 of the lobe, caudally membranous (Fig. 12). Subgenital plates far surpassing tip of pygofer, gradually narrowing, both



Figures 8–18. *Ficiana aurantia* sp. n. **8** forewing **9** hind wing **10** male genitalia, left lateral view **11** pygofer side, left lateral view **12** pygofer, dorsal view **13** anal tube and anal styli, left lateral view **14** aedeagus, left lateral view **15** aedeagus, dorsal view **16** connective **17** paramere **18** subgenital plates. Scale bars: 0.5 mm (**8, 9**); 0.2 mm (**10**); 0.1 mm (**11–18**).

lateral sides curved upwards in lateral view, B-group setae (20–22) near dorsal margin of the plate, arising near base towards subapex in 2-3 rows, C-group setae (8–9) arising in apical 2/5, uniseriate in most part but biseriate near apex, D-group setae sparsely scattered in several irregular rows (Figs 5, 10, 18). Paramere broad and sinuate in most part, with 3 teeth near apex, apically strongly narrowed, long and spine-like, and a

columnar process toward base (Figs 5, 10, 17). Aedeagal in lateral view, shaft tubular, curved and gradually tapering, gonopore apical; dorso-atrium laterally flattened, longer than shaft, with wrinkles and numerous tiny strumae on surface, dorso-basal prolongation bifurcated apically; baso-ventral protrusion of aedeagus longer than the shaft and doratrium in profile, sub-basally strongly curved, apical part broadened and directed dorso-caudally, widest near apex, bearing numerous, bushy setae on the dorsal side; dorsal view, ventro-basal protrusion bifurcated sub-medially, divergent and almost same width in basal 2/3, apices narrowed and curved (Figs 5, 6, 14, 15). Connective closely related to aedeagus near base on dorsal side, posterior and lateral margins concave, anterior margin incised medially (Figs 14–16). Anal tube process strongly narrowing and branched apically, dorsal branch short and tuberculate, ventral branch smooth (Figs 5, 10, 13).

Type material. Holotype. ♂, China, Guangxi, Rongshui, 31 July, 2014, coll. Ye Xu. **Paratypes.** 4 ♂♂, same data as holotype.

Host plants. Unknown.

Etymology. The specific epithet is an adjective derived from the Latin word "*aurantium*", referring to the orange body color of the new species.

Remarks. This new species differs from *Ficiana pruthii* Ghauri by the male pygofer not truncated caudally (Figs 10, 11) (male pygofer truncated caudally in *F. pruthii*); anal tube appendage straight and branched apically (Figs 5, 10, 13) (anal tube appendage curved, not branched apically in *F. pruthii*); paramere spine-like apically, subapex with a short columnar process (Fig. 17) (paramere not spine-like apically, subapically without columnar process in *F. pruthii*).

Distribution. China (Guangxi).

Discussion

Dworakowska (1970) studied the phenomenon of the fusion of the male plates in Cicadellidae. Although Dworakowska supposed this feature is "not rare in Cicadellidae, and it probably cannot say anything about the relationship among the higher taxa". Dworakowska's research still provided some hint for the classification of Empoascini, for the fused plates for some taxa in *Empoasca*-complex seem rather unique and distinguished them from other genera in this tribe. Seven genera, including *Ficiana* Ghauri, *Ishiharella* Dworakowska, *Dialecticopteryx* Kirkaldy, *Mahmoodia* Dworakowska, *Nimabanana* Dworakowska, *Kotwaria* Dworakowska and *Daluana* Ramakrishnan share this feature. Furthermore, all of these genera show some similarities in crown proportions (short and rounded anteriorly, anterior and posterior margins subparallel, middle length distinctly shorter than width between eyes, shared pygofer characteristics (without ventral appendage), the venation of forewing (all apical veins arising from longitudinal m cell) and hind wing (vein CuA unbranched). It is likely that these genera constitute a distinct group (*Ficiana* group) in the process of

evolutionary history and are more closely related than they are to other genera in the *Empoasca*-complex of the tribe.

Ghauri (1963) suggested a resemblance with the genus *Sujitettix* Matsumura and *Kybos* Fieber; however, *Sujitettix* has been treated as a junior synonym of *Apheliona* Kirkaldy by Dworakowska (1970). The genus *Ficiana* is more similar to the six genera noted above. Among these genera, *Ficiana* seems more closely related to *Dialecticopteryx* Kirkaldy, *Nimabanana* Dworakowska, *Kotwaria* Dworakowska and *Daluana* Ramakrishnan in having a distinct coronal suture.

A key to the genera of the *Ficiana* group in the tribe as follows:

Key to genera of *Ficiana* group (males)

1 Coronal suture absent **2**
– Coronal suture present **3**
2 Male pygofer without hook at its upper part; paramere well developed, neither concave nor provided with setae apically (spirally twisted or bifurcated apically) ..... ***Ishiharella* Dworakowska**
– Male pygofer has a well developed hook at its upper part; paramere very feebly developed and provided with setae at their concave tip .... ***Mahmoodia* Dworakowska**
3 Anal tube with baso-ventral processes **4**
– Anal tube without baso-ventral processes **5**
4 Subgenital plates fused from base to subapex, lateral margins slightly convex basally and gradually narrowed apically ..... ***Ficiana* Ghauri**
– Subgenital plates fused only at their bases, lateral margins strongly convex basally and abruptly constricted near mid-length ..... ***Dialecticopteryx* Kirkaldy**
5 Aedeagal shaft with a short ventro-basal and paired slender dorso-basal processes; subgenital plates fused only at their bases ..... ***Nimabanana* Dworakowska**
– Aedeagal shaft simple, without processes; subgenital plates fused in basal 2/3–4/5 ..... **6**
6 Length of vertex, pronotum and scutellum subequal; aedeagus with preatrium; paramere with distinct preapical lobe ..... ***Daluana* Ramakrishnan**
– Length of vertex distinctly shorter than pronotum and scutellum; aedeagus without preatrium; paramere without preapical lobe ..... ***Kotwaria* Dworakowska**

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RESEARCH ARTICLE

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A new species of *Glenochrysa* Esben-Petersen from Australia (Neuroptera, Chrysopidae)

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Abstract

A new species of the charismatic green lacewing genus *Glenochrysa* Esben-Petersen is described from northern Western Australia. *Glenochrysa minima* **sp. n.** represents one of the smallest species of the genus. A key to species of Australian *Glenochrysa* is presented.

Keywords

Green lacewing, Chrysopidae, taxonomy

Introduction

Green lacewings (Neuroptera: Chrysopidae) are a diverse and species rich family with ca. 80 genera comprising over 1200 species in found throughout all major biogeographical regions (Brooks and Barnard 1990). The family is divided into three extant subfamilies, Apochrysinae, Nothochrysinae and Chrysopinae. The majority of the generic and species-level diversity in green lacewings is found in Chrysopinae, which includes approximately 97% of all living species. This subfamily is additionally subdivided into four tribes: Belonopterygini, Chrysopini, Leucochrysini and Ankylopterygini (Brooks and Barnard 1990; Winterton and de Freitas 2006). The most diverse tribe is Chrysopini, with over 40 genera world wide. Many genera in this tribe are nondescript green lacewings with hyaline wings requiring male genitalic dissection to confirm identity, but some are distinctive with

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ornate wing patterns and/or body markings. An example of this is the genus *Glenochrysa* Esben-Petersen, a genus containing 16 species distributed throughout the Afrotropical, Oriental and Australasian regions (Tjeder, 1966; New 1980; Hölzel 1991; Brooks and Barnard 1990; Hölzel and Duelli 2001). A feature characteristic of this genus is the distinctively marked wings, frequently extensive, with additional iridescent embossed pustules on the wing membrane (Brooks and Barnard 1990). Other diagnostic features include in the wing, short Sc vein, meeting the costa before the wing apex, recurrent vein Cu2, and in the male terminalia, tignum and pseudopenis absent, and sternite 8+9 highly modified with medial and lateral projections bearing gonocristae (Tjeder 1966; New 1980; Brooks and Barnard 1990). A spectacular aspect of *Gleochrysa* morphology and biology is the presence of a large prothoracic gland in the male, described as the 'glenofinger' by Duelli (2004) (Fig. 1). While eversible prothoracic glands are known in other Chrysopidae and are used notably for defence (Güsten and Dettner 1991), the shape of this gland and use in males for courtship behaviour is possibly unique to this genus (Duelli 2004). The larva of *Glenochrysa* is a trash carrying type, confirmed in two species, *Glenochrysa ohmi* Holzel & Duelli (Hölzel and Duelli 2001) and *Glenochrysa opposita* (McLachlan) (SLW, unpublished observations).

Five previously described species of *Glenochrysa* are known from Australia (New 1980), all from the eastern state of Queensland: *G. franzeni* Kimmins, *G. tillyardi* New, *G. opposita*, *G. irregularis* (Banks) and *G. regularis* (Banks). A sixth species of *Glenochrysa* is described here from northwestern Australia based on two male specimens. This species is atypical for the genus, due to is unusually small size, but is clearly placed in the genus based on wing and male genitalic characters. A revised key to Australian species of *Glenochrysa* is presented.

Materials and methods

Terminology follows Tjeder (1966) and Brooks & Barnard (1990). Genitalia were macerated in 10% KOH to remove soft tissue, then rinsed in distilled water and dilute glacial acetic acid, dissected in 80% ethanol and subsequently stained with a solution of Chlorazol Black in 40% ethanol. The dissected genitalia were placed in glycerine in a genitalia vial mounted on the pin beneath the specimen.

Taxonomy

***Glenochrysa minima* sp. n.**
http://zoobank.org/64D03B70-AF6C-443B-AE29-E8535F8093DD
Figs 2–4

Type material. Holotype male. **AUSTRALIA**: Western Australia: El Questro-Emma Gorge Resort, 15°54'16.1"S, 128°07'40.7", 20.ix.2002, Whiting, Ogden, Svensen (ANIC).

Figure 1. *Glenochrysa principissa* Navás, male with prothoracic 'glenofinger' gland everted on ceiling in Sihangwana, South Africa, (February, 2002) (from Duelli 2004).

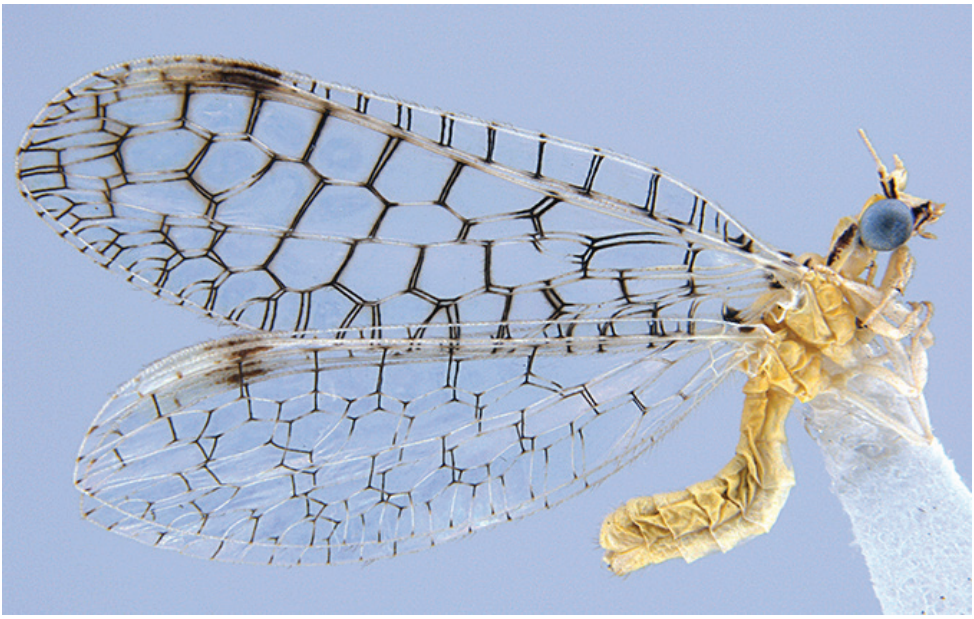

Figure 2. *Glenochrysa minima* sp. n., paratype male habitus. Forewing length = 7.5 mm.

Paratype. male, same data as holotype (CSCA).

Diagnosis. Relatively small species (fore wing length = 7.5 mm); face without band; pronotum with lateral stripe; wing hyaline with dark venation, particularly in forewing;

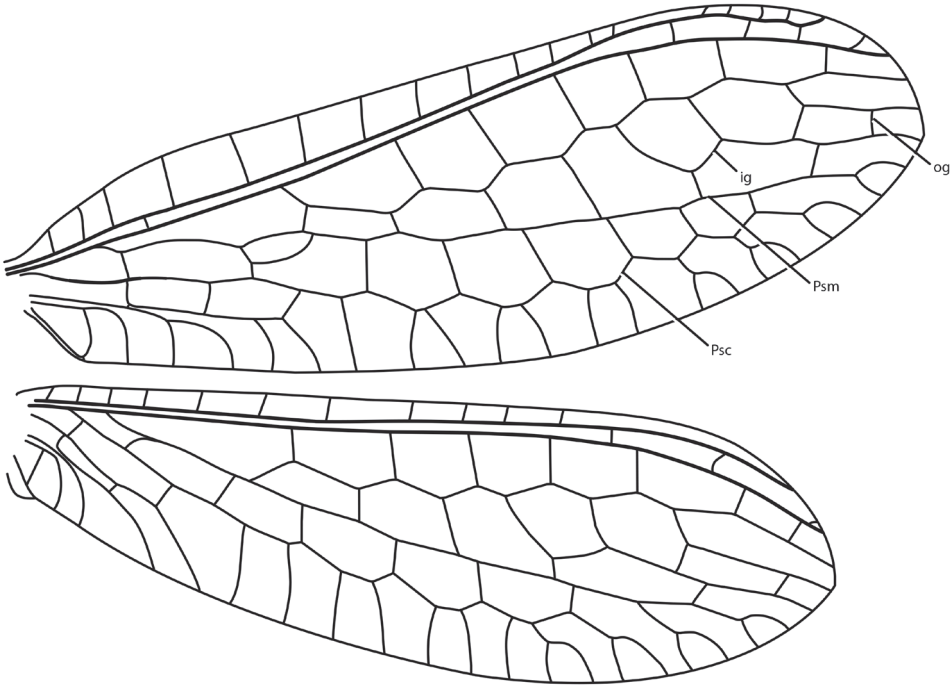

Figure 3. *Glenochrysa minima* sp. n., forewing (upper) and hind wing (lower). Abbreviations: Psc, pseudocubitus; Psm, pseudomedius; ig, inner gradate series; og, outer gradate series. Scale = 7.5 mm.

wings with relatively few crossveins, only two gradates in both the inner and outer gradate series, both gradate series poorly defined; arcessus straight, hooked apically.

Description. Male. Wing length (forewing: 7.5–7.8 mm, hind wing: 4.5 mm) (Figs 2–3). Overall colouration uniform green with black markings on head and thorax; wing membrane mostly unmarked. Head. Yellow, clypeus and frons paler than rest of head; vertex raised, narrow brown mark anteromedially of variable length, from less than half vertex length to full vertex length; palpi unmarked, or sometimes with dark marking laterally on distal segment; frons unmarked; gena and clypeus marked laterally with dark brown-black; small dark brown mark between eye margin and antennal base; antennal scape yellow with two lateral stripes, the anterior stripe slightly wider than the posterior stripe; pedicel yellow with small dark mark laterally; flagellum uniform yellow (broken). Thorax. Prothorax green dorsally, paler on sides, lateral margin with dark brown stripe; anterior margin of prothorax slightly raised where the 'glenofinger' organ is everted; mesothorax yellow-green with dark brown diagonal marking anterolaterally on mesonotum; metathorax entirely yellow-green, unmarked; legs very pale yellow-green, unmarked, base of claw broad; forewing hyaline, longitudinal veins and costal margin largely pale, crossveins dark with narrow infuscation on membrane adjacent to crossveins, more pronounced on first costal crossvein and where vein 3A meeting wing margin; pterostigma dark proximally, pale distally; two

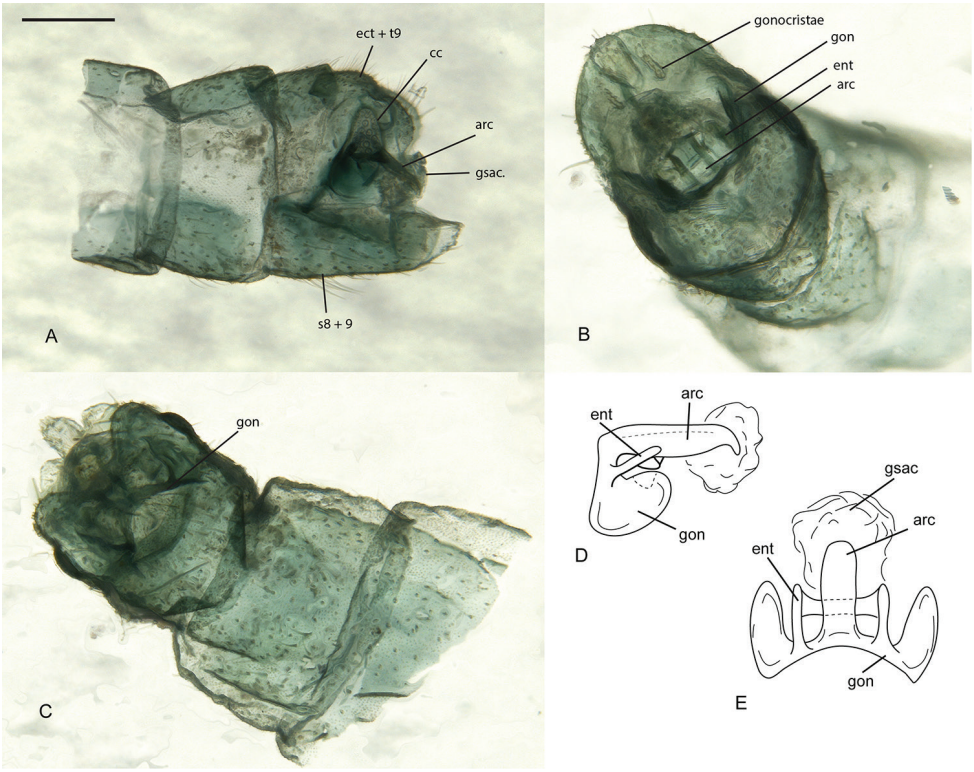

Figure 4. *Glenochrysa minima* sp. n., male terminalia. **A** lateral view **B** posterior view **C** dorsal view **D** gonarcus complex, lateral view **E** gonarcus complex, dorsal view. Abbreviations: ect+t9, ectoproct + tergite 9; cc, cercal callus; arc, arcessus; gsac, gonosaccus; s8+9, sternite 8+9; gon, gonarcus; ent, entoprocessus. Scale bar = 0.2 mm.

widely spaced gradates in each series, with gradates overlapping; inner gradate series not meeting Psm; hindwing similarly hyaline with dark crossveins, although with less intensity and no shading of adjacent membrane; two inner gradates while the outer gradate series differs from one to two between wings. Abdomen. Uniform yellow-green, pale setae present on sclerites of posterior segments; mostly shorter and sparser on anterior segments than rest of abdomen. Genitalia (Fig. 4). Cercal callus with ca. 28 trichobothria and distinct apodeme anteroventrally from cercal callus; ectoproct +tergite 9 broadly rounded in lateral view, inner margin angled in dorsal view, margin with field or erect strong setae posteriorly; sternite 8+9 subquadrangular, posterior margin trilobed with median lobe apex rounded, projecting beyond lateral lobes, lateral lobes with gonocristae along interior margins; gonapsis relatively small; gonarcus arched, arms rounded laterally, entoprocesses rounded, arcessus straight, apex as single lobe, hooked ventrally apically; gonosaccus well developed with uniform gonosetae present.

Female: unknown.

Etymology. The species epithet refers to the diminutive size of this species.

Comments. This new species of *Glenochrysa* is easily distinguished from other species in the genus by the relatively small size, reduced wing venation with few gradates, and limited markings and embossing on the wing membrane.

Revised key to Australian species of *Glenochrysa* Esben-Petersen (after New 1980)

1 Hind wing with conspicuous brown shading ..... ***G. franzeni Kimmins***
– Hind wing unshaded **2**
2 Forewing inner gradates almost transverse, aligned with dark transverse infuscate band ..... ***G. tillyardi* New**
– Forewing inner gradates diagonal, sub-parallel to outer gradates **3**
3 Both forewing and hind wing with two or fewer gradates in both inner and outer gradates series, gradate series poorly defined; 6 (rarely 7) r1-rs crossveins in either forewing or hind wing; forewing venation almost completely dark, wing membrane mostly hyaline except for shading along crossveins; north-western Australia..... ***G. minima* sp. n.**
– Both forewing and hind wing with three or fewer gradates in both inner and outer gradates series, gradate series poorly defined; 8 (rarely 7) r1-rs crossveins in either forewing or hind wing; forewing primary wing veins pale, crossveins darker, infuscate shading in wing membrane; north-eastern Australia **4**
4 Frons and clypeus pale, with black genal mark, sometimes with black crescent like mark below antennal base ..... ***G. opposita* (McLachlan)**
– Frons and clypeus more extensively marked with red **5**
5 Red band across frons; large red mark on gena and onto clypeus .... ***G. irregularis* (Banks)**
– Narrow red band on gena stopping at lateral margin of clypeus, not crossing frons ..... ***G. regularis* (Banks)**

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RESEARCH ARTICLE

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Two new species of *Euptychia* Hübner, 1818 from the upper Amazon basin (Lepidoptera, Nymphalidae, Satyrinae)

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Abstract

Two new species of *Euptychia* Hübner, 1818 are described from the upper Amazon basin: *E. attenboroughi* Neild, Nakahara, Fratello & Le Crom, **sp. n.** (type locality: Amazonas, Venezuela), and *E. sophiae* Zacca, Nakahara, Dolibaina & Dias, **sp. n.** (type locality: Acre, Brazil). Their unusual facies prompted molecular and phylogenetic analyses of one of the species resulting in support for their classification in monophyletic *Euptychia*. Diagnostic characters for the two species are presented based on wing morphology, wing pattern, presence of androconial patches on the hindwing, and genitalia. Our results indicate that the projection of the tegumen above the uncus, previously considered a synapomorphy for *Euptychia*, is not shared by all species in the genus. The adults and their genitalia are documented, and distribution data and a map are provided.

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Resumo

Duas novas espécies de *Euptychia* Hübner, 1818 são descritas da bacia do alto Rio Amazonas: *E. attenboroughi* Neild, Nakahara, Fratello & Le Crom, **sp. n.** (localidade tipo: Amazonas, Venezuela), *E. sophiae* Zacca, Nakahara, Dolibaina & Dias, **sp. n.** (localidade tipo: Acre, Brasil). Suas aparências não usuais levaram a análises molecular e filogenética de uma das espécies que sustentam sua classificação como *Euptychia*. São apresentados caracteres diagnósticos para as duas espécies baseados na morfologia e no padrão de coloração de suas asas, presença de manchas androconiais nas asas posteriores e suas genitálias. Os resultados indicam que a projeção do tegume sobre o unco, previamente considerada uma sinapomorfia para *Euptychia*, não é compartilhada por todas as espécies do gênero. São ilustrados os adultos e suas genitálias, bem como dados e mapa de distribuição.

Resumen

Se describen dos nuevas especies de *Euptychia* Hübner, 1818 para la cuenca alta del Río Amazonas: *E. attenboroughi* Neild, Nakahara, Fratello & Le Crom, **sp. n.** (localidad típica: Amazonas, Venezuela) y *E. sophiae* Zacca, Nakahara, Dolibaina & Dias, **sp. n.** (localidad típica: Acre, Brasil). Sus apariencias inusuales motivaron el análisis molecular y filogenético de una de las especies, lo cual sustenta su clasificación como *Euptychia*. Se presentan caracteres diagnósticos para las dos especies basados en la morfología y patrón de coloración alar, presencia de parches androconiales en las alas posteriores y sus genitales. Los resultados indican que la proyección del tegumen sobre el uncus, previamente considerada una sinapomorfía para *Euptychia*, no es compartida por todas las especies del género. Se ilustran los adultos y sus genitales, y se proporcionan datos y mapa de distribución.

Keywords

Euptychiina, Neotropics, South America, Brazil, Colombia, Peru, Venezuela, mitochondrial DNA COI barcode

Introduction

The nymphalid subtribe Euptychiina (Satyrinae: Satyrini) is one of the most poorly known butterfly groups. More than 400 predominantly Neotropical species in some 50 genera are recognised within the subtribe and many taxa remain undescribed (Lamas 2004; pers. obs.). However, generic classification of species within the subtribe is confused mainly because of a lack of clear morphological characters and morphological homogeneity (Peña and Lamas 2005). In addition, their drab coloration has probably contributed to this group being ignored by many lepidopterists in the field. Forster (1964) described 33 euptychiine genera which are mostly accepted today, but provided few reliable diagnostic characters for these taxa. As a result, placement of species in these genera is often tentative: by way of example, genera such as *Magneuptychia* Forster, 1964, *Cissia* Doubleday, 1848, and *Splendeuptychia* Forster, 1964 are recovered as polyphyletic or paraphyletic in recent phylogenetic analyses (e.g. Peña et al. 2010), indicating the confused generic-level taxonomy. On the other hand, the genus *Euptychia* Hübner, 1818 is relatively well known compared to other euptychiine genera, and is morphologically defined by the posterior projection of the tegumen above the uncus in the male genitalia. This character is considered to be a good synapomorphy (Freitas et

al. 2012) and has been used to classify recently described *Euptychia* species (Neild et al. 2014, Nakahara et al. 2014). Many other described and undescribed *Euptychia* species also possess this character (Nakahara, unpub.), and its presence even contributed to the inclusion of *Caenoptychia boulleti* Le Cerf, 1919 in *Euptychia* (Freitas et al. 2012). However, we here describe two new species of *Euptychia* which lack this posterior projection of the tegumen. The placement of these two species in *Euptychia* is supported by molecular data, which are presented in this paper, and by many alternative possible diagnostic characters for the genus, which are discussed.

Methods

Morphology

Comparison of the morphology of the two new species was made with other *Euptychia* specimens in the collections listed below (museum acronyms are from Heppner and Lamas 1982):

AMNH American Museum of Natural History, New York, USA
AN Andrew Neild collection, London, UK
BMNH The Natural History Museum, London, UK
DZUP Coleção Entomológica Padre Jesus de Santiago Moure, Universidade Federal do Paraná, Curitiba, Brazil
ICN-MHN-L Instituto de Ciencias Naturales, Colección de Lepidoptera, Universidad Nacional de Colombia, Bogotá, Colombia
MGCL McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, USA
MUSM Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru

Type specimens of *Euptychia* species in the BMNH were also checked, as well as photographs of additional taxa on the website "Butterflies of America" (available online in Warren et al. 2015). In addition, recent works on French Guianan *Euptychia* by Brévignon (2005, 2008) and Brévignon and Benmesbah (2012) were consulted, and our taxa were discussed with the authors of those papers. Wings were diaphanised using standard techniques for Lepidoptera. The abdomens of the Venezuelan pair of *E. attenboroughi* sp. n. and one of the Brazilian males of *E. sophiae* sp. n. were dissected to observe genital structures. Abdomens were dissected using standard techniques, with adult abdomens being soaked in hot 10% KOH solution for 3–10 minutes, dissected and subsequently stored in microvials in glycerine. External morphology and dissections were studied using stereomicroscopes and photographed using digital cameras. The terminology for genital and abdominal structures follows Scoble (1992), with additional detail derived from Klots (1956). Our use of the term "vinculum" agrees

with Austin and Mielke (2008). Nomenclature for wing venation corresponds to that of Miller (1970: 46), and wing areas to Neild (2008: fig. 1.2).

The following abbreviations are used:

FW forewing
HW hindwing
D dorsal
V ventral

Molecular and phylogenetic analysis

A leg from the Brazilian male paratype (DZ 29.578) of *E. sophiae* sp. n. was used to obtain a DNA sequence for cytochrome c oxidase subunit I (COI) and elongation factor-1 alpha (ef1a). We extracted DNA using Qiagen's DNeasy Blood & Tissue Kit, following the protocol and using a final elution volume of 50 µl. Primers LCO_nym (forward, 5'TTTCTACAAATCATAAAGATATTGG 3') and HCO_nym (reverse, 5'TAAACTTCAGGGGTGACCAAAAAATCA 3') were used to amplify COI. Elongation factor-1 alpha was amplified by using primer pairs Ef44 (forward, 5'GCYGARCGYGARCGTGGTATYAC 3'), and EfrcM4 (reverse, 5'ACAGCVACKGTYTGYCTCATRTC 3'); however, since this primer pair failed to amplify ef1a, the following primer pair was used to amplify short fragments of ef1a: Ef44 (forward, 5'GCYGARCGYGARCGTGGTATYAC 3') and Monica (reverse, 5'CATRTTGTCKCCGTGCCARCC 3') (Monteiro and Pierce 2001). All PCR reactions were conducted in a 25 µl volume comprising 1 µl of template DNA, 9.5 µl ddH2O, 1 µl of each primer (10 µM), and 12.5 µl Omega 2x Taq Mastermix (Omega Bio-tek, Norcross, GA, USA) (5 U/µl). Reaction conditions were as follows: for COI, 1 min at 94 °C, followed by 5 cycles of 30 s at 94 °C, 40 s at 45 °C, 1 min at 72 °C, followed by 35 cycles of 30 s at 94 °C, 40 s at 51 °C, 1 min at 72 °C, followed by final elongation for 5 min at 72 °C; for Ef1a, 35 cycles of 1 min at 95 °C, 1 min at 58 °C, and 1 min at 72 °C, followed by final extension for 5 min at 72 °C; for short fragment of Ef1a, 1 min at 95 °C, 40 cycles of 30 s at 94 °C, 40 s at 58 °C, and 1 min at 72 °C, followed by final extension for 5 min at 72 °C. PCR products were checked on 1.2% agarose gels stained with ethidium bromide. Purification and sequencing were completed at the Interdisciplinary Center for Biotechnology Research (ICBR) at the University of Florida. Two sequences were uploaded to GenBank (KR818703, KR818706) and were analysed with 8 other *Euptychia* species and 2 outgroup taxa from GenBank (see Table 1).

Sequences were aligned using MAFFT v. 7.107 (Katoh et al. 2002). Best-fitting models and partitioning schemes were jointly selected using PartitionFinder v. 1.1.1. (Lanfear et al. 2012). The program was run twice, once with the models available in MrBayes 3.2.3 (Ronquist et al. 2012) and once with those in RAxML v. 8.1.11 (Stamatakis 2006). The selected partitioning schemes and models can be found in Table 2.

Table 1. GenBank accession numbers for sequences used in this study.

Genus	Species	Voucher code	COI	EF1a
Euptychia	*enyo*	CP06-73	GQ357205	GQ357275
Euptychia	sp. 2	CP01-33	DQ338794	DQ338937
Euptychia	*westwoodi*	DNA96-005	AY508543	AY509069
Euptychia	*boulleti*	PM17-01	JQ639284	JQ639285
Euptychia	sp. 6	CP04-55	DQ338796	DQ338939
Euptychia	*sophiae*	DZ 29.578	KR818703	KR818706
Euptychia	*picea*	DNA99-036	AY508542	AY509068
Euptychia	sp. 5	CP01-53	DQ338795	DQ338938
Euptychia	sp. 7	CP02-58	GQ357206	DQ338940
Magneuptychia	*fugitiva*	CP01-18 / DNA99-008	GU205845	AY509078
Papilio	*machaon*	BC ZSMLep 27060 / NA	GU707119	EF485106

Table 2. Partitioning schemes and substitution models determined by Partitionfinder.

Partition	Best model MrBayes	Subset partitions BEAST	Best model RAxML	Subset partitions RAxML
1	GTR+I	COI position 1	GTR	COI position 1
2	HKY+I	COI position 2	GTR	COI position 2
3	HKY+G	COI position 3	GTR	COI position 3
4	GTR	EF1a position 1	GTR	EF1a position 1
5	HKY	EF1a position 2	GTR	EF1a position 2
6	GTR+G	EF1a position 3	GTR	EF1a position 3

Phylogenies were inferred using maximum likelihood (ML) and Bayesian inference on the concatenated data set of 1041bp. ML analyses were run using RAxML v 8.1.11 (Stamatakis 2006, Stamatakis et al. 2008) with the GTR model for all partitions (as selected by PartitionFinder) and 1000 rapid bootstrap replicates followed by 200 thorough maximum likelihood searches with joint branch length optimization. Bayesian analyses were run in MrBayes 3.2.3. Analyses were run twice for 10 million generations with trees sampled every 1000 generations with the temperature parameter set to 0.15. Model parameters were unlinked across data partitions, and the prior for rate variation among partitions was set to variable. The first 25% of the samples were discarded as burn-in. Convergence was checked in Tracer 1.6 (Rambaut and Drummond 2007). RAxML and MrBayes were run on the CIPRES cluster (Miller et al. 2010).

Results

According to ML and Bayesian inference based on barcoding region and EF1a, *E. sophiae* sp. n. is sister to the clade consisting of *E. picea* Butler, 1867 and two undescribed species. Unlike Freitas et al. (2012), *Euptychia boulleti* (Le Cerf, 1919) is here placed as sister to the clade with *E. enyo* Butler, 1867, *E. westwoodi* Butler, 1867, and

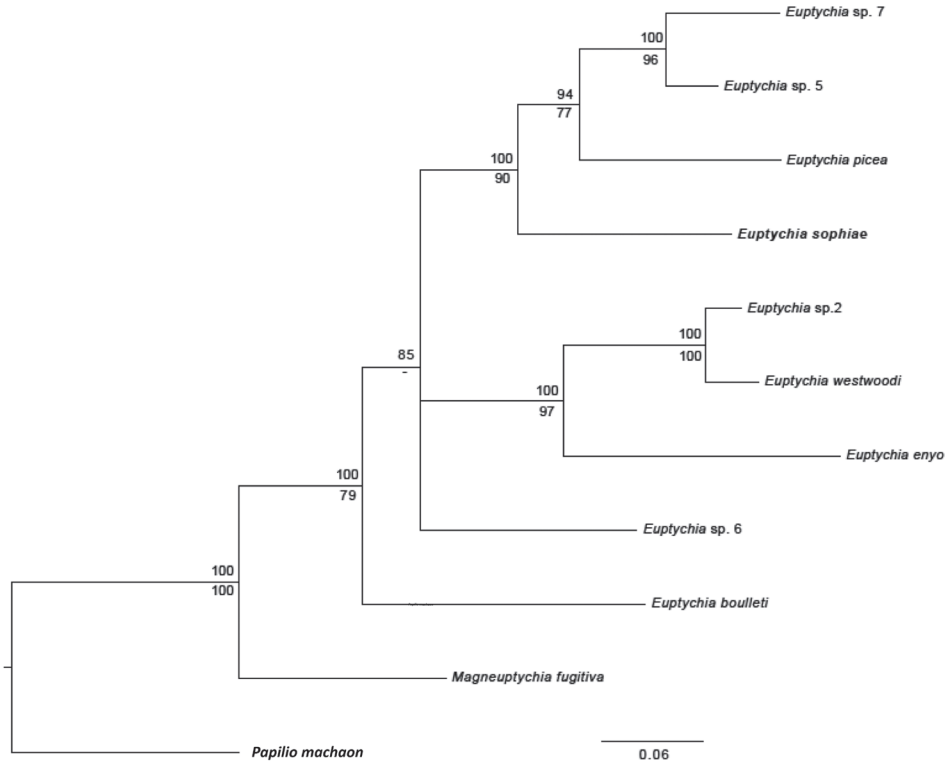


Figure 1. Bayesian phylogeny of *Euptychia* based on one mitochondrial (COI) and one nuclear (EF1-a) gene. Posterior probabilities are listed above and bootstrap values below branches. A dash denotes bootstrap support lower than 50%. (*Euptychia attenboroughi* is not included in the analysis – see text for details.)

an undescribed species in the ML tree, although with relatively low support. However, in the Bayesian tree (Fig. 1), this species appears as sister to the rest of *Euptychia*. Thus in this tree the ancestor of *Euptychia* (minus *E. boulleti*) has no bootstrap support since this node does not exist in the ML tree. Placement of *E. sophiae* sp. n. in monophyletic *Euptychia* is supported by both analyses. The results of this molecular analysis are supported by the ML analysis in Nakahara et al. (2015), which included over 150 euptychiine and other satyrine taxa and recovered the genus *Euptychia* as monophyletic and including *E. sophiae* (as *Euptychia*_n_sp).

Taxonomy

Diagnostic morphological characters seen in these two new species which appear to be unique among the genus *Euptychia* include: (i) presence of a single signum in female *E. attenboroughi* sp. n. (no female is known for *E. sophiae* sp. n.); (ii) lamella antevaginalis

unsclerotised around the ostium bursae of female *E. attenboroughi* sp. n. (sclerotised in all other *Euptychia* examined), except on the ventral surface around the neck of the ostium bursae; (iii) reduced third segment of labial palpus of female *E. attenboroughi* sp. n. (Fig. 5); (iv) presence of a prominent ventral hindwing androconial patch in male *E. sophiae* sp. n. None of these characters are known in any other species of *Euptychia* we have examined and are considered to be diagnostic for *E. attenboroughi* sp. n. (states i, ii and iii) and *E. sophiae* sp. n. (state iv). For diagnostic characters for *E. attenboroughi* sp. n. and *E. sophiae* sp. n., consult the diagnosis for each species.

***Euptychia attenboroughi* Neild, Nakahara, Fratello & Le Crom, sp. n.**
http://zoobank.org/FA31E137-39EC-4B26-B9E8-48E7F4032773
Figs 2–6; Map 1

Type material. Holotype male with the following labels (separated by transverse bars): HOLOTYPE / VENEZUELA – *Amazonas*: San Carlos de Rio Negro to Solano track, km. 3 [approximately 1°55'N 67°1'W], 5-17 III 94, 100m elev., Andrew Neild Collection / Brit. Mus. 1994-298 / BMNH(E) #1054424 (BMNH).

Paratypes. VENEZUELA – *Amazonas*: 1 female, same locality data as holotype / (Neild Prep. Genital Vial No. 274) (AN); BRAZIL – *Amazonas*: 1 female, Janarete [= Jauaretê] (approximately 0°36'N 69°11'W), IX, 1943 / W. Praetorius Coll. Donor Frank Johnson (AMNH); COLOMBIA – *Vaupés*: 1 male, Camino a mina "La Libertad", camino a caño grande "Pescadero", en bosque amazónico [approximately 1°01'N 69°45'W, north of Chorro La Libertad, *fide* Jaime Pinzón], 10:30 am, 290 m, 25-Agosto-1993, Col: G. Fagua (ICN-MHN-L); 1 female, Serranía de Taraira; camino a mina "La Libertad", camino a mina "Marulanda"; en rastrojo [approximately 1°01'N 69°45'W, north of Chorro La Libertad, *fide* Jaime Pinzón], 2:45pm, 290 m, 8 agosto 1993, G. Fagua (ICN-MHN-L); *No data*: 1 male, (genital vial # SN-15-59) (MGCL).

Diagnosis. Differs from males of its congener *E. sophiae* sp. n. as follows (no females of *E. sophiae* sp. n. are known, but we expect characters indicated with an asterisk (*) will serve to differentiate this sex): (1) FW more produced apically, with outer margin straighter or more concave, and outer margin at an angle away from the central line of the body (nearly parallel in *E. sophiae* sp. n.); (2) dorsally with prominent orange scaling on the posterior DHW on and near the tornus* (*E. sophiae* sp. n. lacks this orange scaling); (3) VHW submarginal band does not increase in width at the tornus (increases substantially for *E. sophiae* sp. n.); (4) small ocellus at the anal margin of the VHW median band larger*; (5) androconial patch on VHW pale and barely visible, whereas prominent on *E. sophiae* sp. n.; (6) gnathos projecting nearly parallel to the uncus (projecting vertically in *E. sophiae* sp. n.); (7) distal one-fourth of the valva broad in lateral view (narrow in *E. sophiae* sp. n.); (8) aedeagus straighter, less curved.

The female resembles several species in the genus *Euptychia*, especially *E. marceli* Brévignon, 2005, but is distinguishable on the VHW through the unique combination of a very large and ovoid (not round) ocellus in Cu_1-Cu_2 bordered on its tornal

side by orange scaling, and by the presence of a tiny ocellus on the anal margin at the posterior end of the median brown band (this last found rarely on some specimens of *E. marceli* Brévignon, 2005). It can also be differentiated from all other known *Euptychia* females by the three characters (i, ii, and iii) elucidated at the beginning of the Taxonomy section. The male somewhat resembles a few taxa currently in *Chloreuptychia* Forster, 1964 (see Warren et al. 2015), with its wing shape and greyish translucence, but differs by the absence of a bluish sheen on either wing surface, presence of orange HW tornal scaling on both wing surfaces, presence of a small VHW ocellus at the anal margin, absence of orange- and silver-lined ovoid VHW markings in M_2-M_3 and M_3-Cu_1, and by the single silvery-white pupils in the VHW ocelli (double in most *Chloreuptychia* species).

Description. MALE (Fig. 2):

Forewing length. 17.0–18.0 mm (n = 3) (holotype = 18 mm).

Head. Frons brownish; postgenal area light brown.

Antennae. Naked, orange-brown, darker dorsally, clubs browner with orange tip, 7–8 mm long.

Eyes. Dark brown, sparsely hairy; creamy-grey scales dorsally and laterally along posterior edge of eyes.

Palpi. Covered by long creamy-grey hair-like modified scales dorso-laterally, ventrally with long fine hair-like modified scales projecting like a Mohican, mostly black along outer margin, but interior wall of modified scales creamy-grey. Mohican highest in centre, gradually reducing anteriorly and posteriorly, and anteriorly reduced to a pointed tuft. First segment covered with black scales dorsally, black and white hair-like modified scales ventrally, second segment covered with short white hair-like modified scales and white scales laterally, black scales distal one-third of dorsal surface, ventrally adorned with long black and white hair-like modified scales 3–4 times as long as segment width, second segment slightly longer than eye diameter, third segment covered with black scales dorsally and ventrally, creamy-white hair-like scales laterally, about one-seventh of second segment in length.

Thorax. Covered in long light grey hair-like modified scales.

Legs. Greyish. Foreleg tarsus about 2/5 of tibia in length, femur about 2/3 of tibia in length; tibial spurs absent on midleg and hindleg.

Abdomen. Eighth tergite and sternite well developed, apparently as equally sclerotized as other tergites and sternites, but weakly sclerotized towards posterior end.

Androconia patches. Modified wing scales, presumed to be androconia, present on either side of vein 2A on the HW at the base of the dark median band on the dorsal and ventral surface; visible on the dorsal surface as two tiny ovoid pale greyish-brown patches approximately 0.5 mm long, and on the ventral surface as a strip approximately 2.0 mm long in space 2A–3A; these patches, best viewed using backlighting, are homologous with the dorsal and ventral androconia patches of *E. sophiae* sp. n.

Wing venation. FW recurrent vein present, approximately 1.75 mm long; FW vein Cu not swollen at base; HW with humeral vein barely visible, very short (approximately 0.6 mm), curved anteriorly towards the costal lobe.

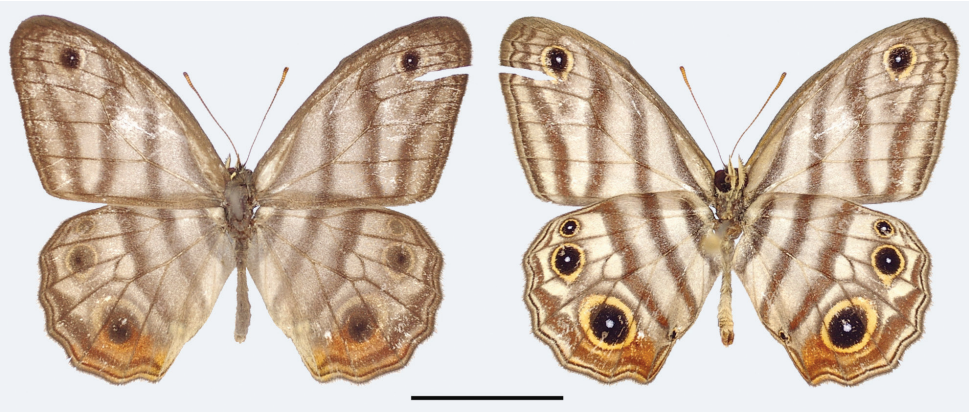


Figure 2. *Euptychia attenboroughi* sp. n. holotype male, dorsal (left) and ventral (right). FW length: 18.0 mm. BMNH collection. Photos by Andrew Neild, Trustees of the Natural History Museum, London. Scale bar: 10 mm.

Wing shape. FW costa gently convex to apex, apex relatively pointed, outer margin straight, or slightly concave between M_3 and Cu_2, and angling about 20 degrees away from the central line of the body, inner margin almost straight; HW costa lobed in basal area then gently concave to apex at $Sc+R_1$, apex rounded, outer margin scalloped, anal margin concave near tornus, basally convex.

DFW. Both wings slightly and variably translucent with greyish-brown to chestnut brown ground colour; fringes greyish-brown to brown; four diffuse dark brown to chestnut bands crossing from the costal to the anal margin, the first basal and barely visible, mostly ghosting through the slightly translucent wing from the ventral surface, centrally wide but tapering to a point anteriorly and posteriorly, the second submedian, wider, nearly straight and better defined, crosses the mid discal cell from mid costa to four tenths along the inner margin, the third median slightly wavy strongly defined and the widest, crosses from the costa near the discocellular veins, which it traverses, reaching to seven tenths distance along the inner margin, the fourth begins near the apex where it is narrow and very sinuous, runs parallel to the outer margin and curved in each interspace down to M_3 and then angles without curves in towards the body and widens reaching the submarginal area of Cu_1, then again running parallel to the outer margin down to the inner margin near the tornus; the margin with a very fine dark brown line running parallel to the outer margin, beginning at the apex, incurved in each interspace to M_3, then straight to the tornus; a white-pupilled black subapical ocellus in the centre of M_1-M_2, touching M_2 but not quite reaching M_1.

DHW. Four diffuse dark brown to chestnut bands crossing from the costal to the anal margin, the first basal, mostly ghosting through the slightly translucent wing from the ventral surface, the second submedian also ghosting through, nearly straight, crosses the mid discal cell from mid costa to half distance along the anal margin, the third median and slightly wavy, in some specimens (two of the three males) curved

inwards in the distal discal cell, better defined with dorsal scaling (less ghosting) and the widest, crosses from the costa two-thirds towards the apex, almost reaching 2A two-thirds along its length, and not passing to the anal margin, the fourth submarginal begins near the apex where it is narrow, runs parallel to the outer margin (curved in each interspace), gradually thickening, widest in M_2-M_3 (where the basal edge points inward) and M_3-Cu_1, and then thinning gradually to just reach 2A near the tornus; the margin with a very fine clearly defined dark brown line running parallel to the outer margin, beginning at Sc+R_1, incurved in each interspace to the tornus and entering the anal lobe to 3A; three ventral ocelli visible through the slightly translucent wings, the dark circular areas showing through from the ventral surface in cells Cu_1-Cu_2 and M_1-M_2 covered with small spheroid areas of diffuse very dark brown dorsal scaling, the latter very small, the former roughly half the diameter of the black ventral "iris"; orange scaling on the distal side of the large ocellus in space Cu_1-Cu_2 continues to the outer margin and in the same areas of Cu_2-2A.

VFW. Both wings slightly translucent with pale greyish-brown ground colour; fringes greyish-brown; one very thin well-defined submarginal dark brown to chestnut band and four more diffuse dark brown to chestnut basal bands, submedian, median and postmedian crossing from the costal to the anal margin, as described for the dorsal surface; a silvery-white-pupilled black subapical ocellus in the centre of space M_1-M_2, touching M_2 but not quite reaching M_1, circled by a gold ring with a thin grey-brown outer edge which enters R_5-M_1; in M_2-M_3 the grey-brown edge of the ocellar ring breaks open and the yellow area spills posteriorly into the centre of the interspace; in one specimen (MGCL) there is an additional tiny ocellus in Cu_1-Cu_2 with a reddish-brown "iris" (of the same colour as the transverse bands), a tiny pupil (or merely missing scales?), and an outer ring of the same colour as the background pale-grey-brown, surrounded by an indistinct scattering of brownish scales that define the edge of the outer pale ring.

VHW. One very thin well-defined marginal dark brown band and four more diffuse dark brown to chestnut basal bands, submedian, median, and marginal crossing from the costal to the anal margin, as described for the dorsal surface, but the submarginal and marginal bands continue from the tornus along the anal margin to the base of the chestnut median band, while the marginal band (only) continues to the base of the submedian band; a very small ocellus on the anal margin at the base of the median brown band composed of a large black subovoid "iris", a narrow golden outer ring, and a narrow dark brown border; three postmedian ocelli, composed of a single small silvery-white pupil, a large black spheroid or ovoid "iris", and a narrow golden outer ring enclosed in a narrow grey-brown border; the smallest of these ocelli is spheroid, entirely within Rs-M_1, not touching either vein, the second, nearly twice as large, spheroid and occupying the full width of M_1-M_2, with the grey-brown outer border just touching M_1, and the black "iris" just spilling over into M_2-M_3, and in the same way as on the VFW, with the outer posterior border broken open in M_2-M_3 and the golden outer ring protruding into the centre of the interspace, where a poorly defined wide suffused band of greyish brown scales links this and the third largest ocellus,

ovoid, over three times the diameter of the first at its widest point (parallel to the outer margin), with the black "iris" fully occupying Cu_1-Cu_2, spilling into M_3-Cu_1 but just touching Cu_2, the golden outer ring double the width of the other two ocelli, reaching the centre of M_3-Cu_1, and entering Cu_2-2A, surrounded by a grey brown ring with indistinct edges; yellow-orange scaling on the distal side of the large ocellus in space Cu_1-Cu_2 continues slightly into M_3-Cu_1 and fully to the submarginal band of Cu_1-Cu_2 with more extensive orange scaling in the distal quarter of Cu_2-2A just spilling over 2A onto the anal lobe.

Male genitalia (Fig. 4). Tegumen dorsally flattened, ventral edges concave, posterior margin projecting to form a short gnathos fused to the tegumen (approximately one-fifth length of uncus) almost parallel to uncus, but slightly ventrad, somewhat trapezoid in dorsal view; uncus anteriorly hairy, rather narrow and long, posterior tapered and slightly hooked in lateral view, evenly wide in dorsal view; ventral arms of tegumen fused to anterior margin of tegumen; appendices angulares absent; saccus slightly longer than uncus, dorsal arms of saccus combined with ventral arms from tegumen; valva sparsely hairy, basal three-fourths vaguely trapezoidal, distal one-fourth rounded, distal half of valva in dorso-ventral view resembles propodus of a lobster, but without the dactylus; aedeagus tubular, in lateral view rather straight, slightly broadening anterior portion which opens anterodorsally, posterior one third of aedeagus narrow, slightly bent upwards, cornuti absent.

FEMALE (Fig. 3):

Forewing length 16.0–17.0 mm (n = 3). Similar to male except as follows: FW shape not elongate, subtriangular, with distinctly convex outer margin; HW shape similar to male, but slightly less elongate; dorsal surface with all the same dark semi-translucent bands but the basal, submedian, and median bands with more scales present dorsally; the DHW dark circular areas showing through from the ventral surface in cells Cu_1-Cu_2 and M_1-M_2 almost covered with large spheroid areas of diffuse very dark brown, nearly black, dorsal scaling; the large subtornal ocellus entirely encircled

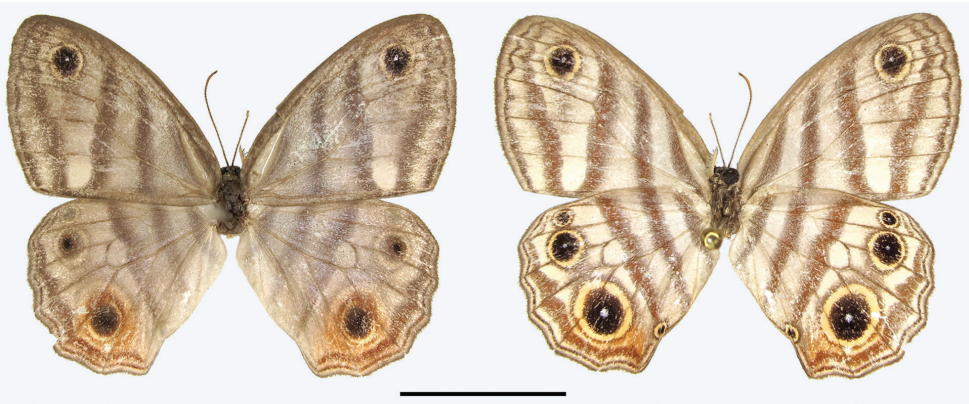


Figure 3. *Euptychia attenboroughi* sp. n. paratype female, dorsal (left) and ventral (right). FW length: 16.0 mm. AN collection. Photos by Andrew Neild. Scale bar: 10 mm.

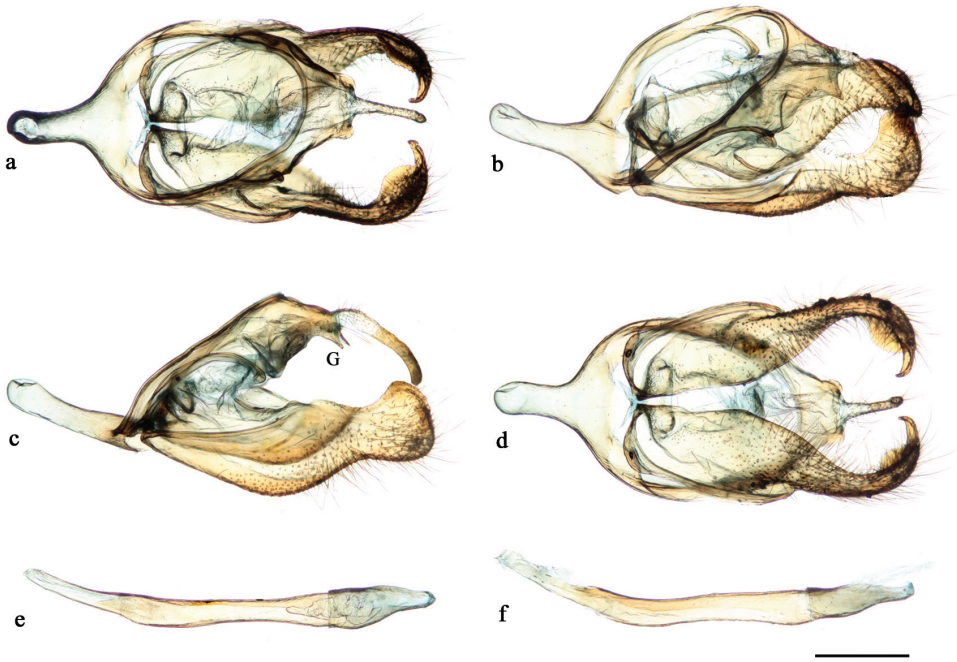


Figure 4. *Euptychia attenboroughi* sp. n. Genitalia of holotype male: **a** dorsal view **b** dorso-lateral view **c** lateral view ("G" indicates fused gnathos) **d** ventral view **e** aedeagus, dorsal view, and **f** lateral view. BMNH collection. Photos by Andrew Neild, Trustees of the Natural History Museum, London. Scale bar: 0.5 mm.

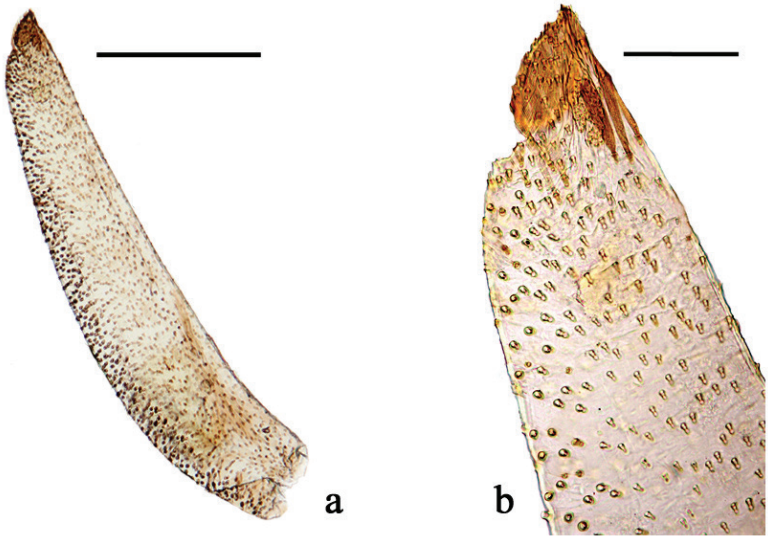


Figure 5. *Euptychia attenboroughi* sp. n. Left labial palpus of paratype female: **a** lateral view of second and third segment **b** detail of second and third segment. AN collection. Photos by Andrew Neild. Scale bar: 0.5 mm (**a**), 0.1 mm (**b**)

Figure 6. *Euptychia attenboroughi* sp. n. Genitalia of paratype female: postero-ventral view. AN collection. Photos by Andrew Neild. Scale bar: 0.5 mm.

by diffuse orange scaling, and distally by a half-circle of golden scales homologous with the ventral outer ring of this colour; ventrally there are no obvious differences.

Female genitalia (Fig. 6). One Venezuelan female was examined (Neild Prep. Genital Vial No. 274). Lamella antevaginalis sclerotized; area around lamella antevaginalis not sclerotized; very basal side of 8th abdominal segment slightly sclerotized and somewhat ring-like at basal side of 8th abdominal segments; ductus bursae membranous; ductus seminalis located near ostium bursae; corpus bursae oval in dorsal view, with one relatively thick signum.

Etymology. We name this butterfly to honour the great English naturalist, author, and TV presenter, Sir David Attenborough, in gratitude for opening the eyes and hearts of millions to the natural world through his inspiring and edifying work. To prevent any future ambiguity, the name *attenboroughi* is considered to be a Latinised male noun in the genitive case.

Distribution, behaviour and habitat. The six specimens known to date were all collected within 500 kms of each other in the north-west of the upper Amazon basin, representing a very restricted distribution. It is impossible with such a small sample size to draw any concrete conclusions, but we hypothesise that this species is restricted to suitable habitat to the north of the Amazon river, and that its sibling species occurs only to the south, although a limited area of sympatry may exist. One of the senior authors first collected specimens of this new species in 1994 while conducting field work for the *Butterflies of Venezuela* book series (Neild 1996, Neild 2008) in south-western Venezuela. The pair that he collected were settled on low vegetation along a path inside tropical evergreen forest and were netted immediately, before any further observations could be made. One of the Colombian specimens was collected in similar habitat at 10:30 a.m., while the female was captured at 2:45pm outside the forest in scrubby secondary vegetation ("*rastrojo*"). The type series were all found at low elevations from about 100 m to almost 300 m above sea level. The two Venezuelan specimens were collected in the first half of March, during an especially strong dry season which drastically reduced butterfly numbers and species diversity. The Colombian and Brazilian specimens were taken in August and September, months that are also typically among the least wet of the year. The species is evidently very rarely collected, but this may not reflect reality in the field; rather its perceived scarcity may simply be the result of its apparently highly restricted distribution in an area of the Amazon basin that has been, and still is, very little explored.

Host plant. Unknown.

Euptychia sophiae Zacca, Nakahara, Dolibaina & Dias, sp. n.

http://zoobank.org/F81B7816-4C91-4A9B-9105-AD1F3D9F603C
Figs 7, 8; Map 1

Type material. Holotype male with the following labels (separated by transverse bars): /Holotypus/ Brasil, Acre, Mâncio Lima, P[ar]q[ue] Nac[ional] Serra Do Divisor, Porção Norte, 7°26'50"S 73°39'52"W 200-400 m 10-21-IX-2011, D. Dolibaina & D. Moura Leg. / DZ 29.579/ (DZUP).

Paratype. 1 male, same data as holotype, except: DZ 29.578 (DZUP); PERU – *Loreto*: 1 male, 45 km. E. de Monte Alegre, Rio Trapiche [rec. Tapiche], 73°47'39.51"S 6°22'58.43"W [*sic* – W and S are transposed], 19–20.ii.2009, 183m, A. Garcia *leg.* (MUSM).

Diagnosis. See relevant section for *E. attenboroughi*.

Description. MALE (Fig. 7):

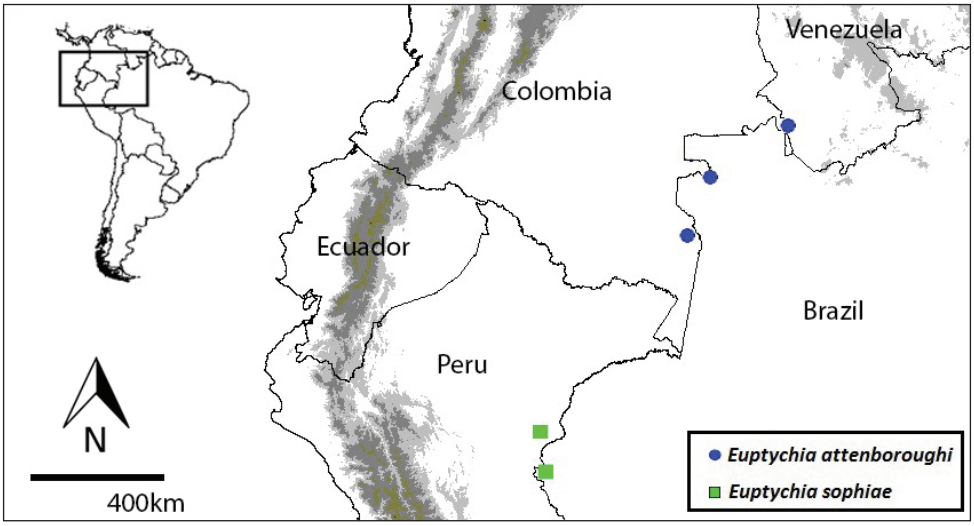
Forewing length 18–19 mm (n = 3) (holotype = 18 mm).

Head. Brown. Postgenae with creamy-grey scales.

Antennae. Naked, brown, darker dorsally, clubs browner with orange tip.

Eyes. Dark brown, sparsely hairy. Creamy-grey scales dorsally and laterally along posterior edge of eyes.

Palpi. Covered by long creamy-grey hair-like modified scales dorso-laterally, ventrally with long fine hair-like modified scales projecting like a Mohican, mostly black



Map 1. Distribution of *Euptychia attenboroughi* sp. n. (blue circles) and *E. sophiae* sp. n. (green squares).

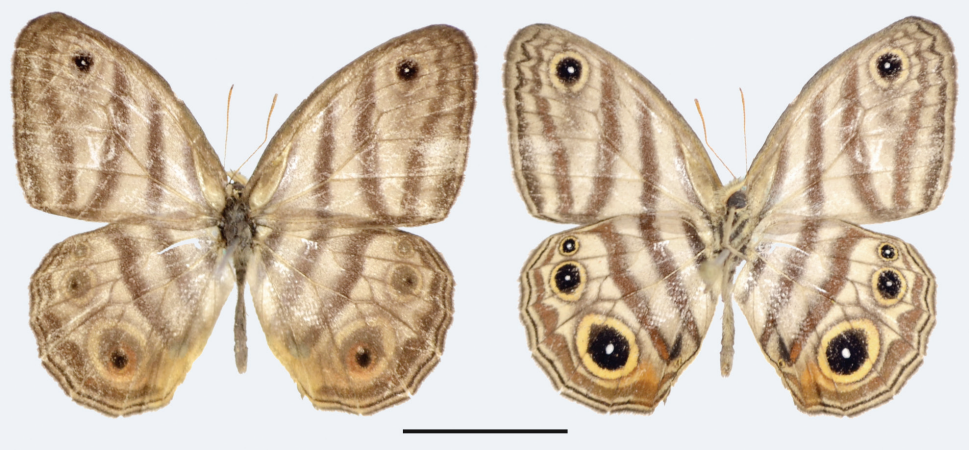


Figure 7. *Euptychia sophiae* sp. n. holotype male, dorsal (left) and ventral (right). FW length: 18.0 mm. DZUP collection. Photos by Thamara Zacca. Scale bar: 10 mm.

along outer margin, but interior wall of modified scales creamy-grey. Mohican highest in centre, gradually reducing anteriorly and posteriorly, and anteriorly reduced to a pointed tuft. First segment covered with brown scales dorsally, black and creamy hair-like modified scales ventrally, second segment covered with short creamy hair-like modified scales and light brown scales laterally, brown scales distal one-third of dorsal surface, ventrally adorned with long black and creamy hair-like modified scales 3–4 times as long as segment width, second segment slightly longer than eye diameter, third segment covered with brown scales dorsally and black scales ventrally, creamy hair-like scales laterally, about one-seventh of second segment in length.

Thorax. Uniformly covered by dark grey-brown hair-like scales.

Legs. Greyish. Foreleg tarsus more than half-length of tibia, femur about 2/3 of tibia in length; tibial spurs absent on midleg and hindleg.

Abdomen. Eighth tergite and sternite well developed, apparently as equally sclerotized as other tergites and sternites, but weakly sclerotized towards posterior end.

Androconial patches. Two small (< 1.0 mm) pale grey androconial patches on DHW, barely separated by 2A, located at its distal one third; patch in cell 2A–3A prominent; patch in cell Cu_1-Cu_2 restricted to width of median band and located at juncture of this band with 2A. A black and short (approximately 1.5–2.0 mm) androconial patch at the distal third of 2A on the VHW.

Wing shape. FW triangular, costal margin convex, apex rounded, outer margin gently convex from apex to Cu_1, tornus rounded, anal margin straight. VW costa slightly convex, apex rounded, outer margin crenulated, anal margin concave near tornus, remaining convex.

DFW. Greyish brown, darker along the costal and outer margins with a narrow ochre area on the first fourth of the costal margin length. Four dark brown to rufous bands, the former basal, dark brown (approximately 0.1 mm width) following the radial vein on its distal edge, the second submedian, dark rufous brown, from near the origin of R_1 to 2A, crossing the discal cell near the middle, the third median, rufous and slightly concave, crossing the cell end from the origin of R_3 across the base of Cu_1 to 2A, curving distally near the inner margin, and the final band submarginal, dark brown, narrower and slightly crenulated from R_4 to M_3, rufous and posteriorly enlarged from M_3 to 2A. Ocellus of the VFW observable through transparency.

DHW. Greyish brown. Four dark brown to rufous straight bands, the first basal, dark brown, short and tapered, the second submedian, dark rufous brown, from costal margin to anal margin, crossing the discal cell near the centre, the third median, rufous brown, from costal margin to anal margin, crossing the discal cell in its distal quarter, the final band submarginal, rufous and crenulated in each cell from Rs to anal margin, except Cu_1-Cu_2, following the contour of the outer margin, but widened and curved inwards in M_2-M_3 and to a lesser degree in M_3-Cu_1, wide and reddish orange from Cu_1 to 2A, thinned from 2A to anal margin where it nearly reaches the median rufous band. Ocelli of the VHW observable through transparency.

VFW. Light greyish brown, bands similar to DFW. One developed black ocellus from M_1 to anterior sixth in M_2-M_3, with a white pupil at the centre and a broad and yellow external ring, surrounded by a greyish brown area that extends posteriorly to the posterior half of M_3-Cu_1. Submarginal line dark brown, from R_4 to anal margin, crenulated in R_4-M_3, remainder and straight, distally surrounded by a thin yellow line. Fringes dark brown.

VHW. Light greyish brown, bands similar to DHW. Three postmedian black ocelli, the anterior the smallest in Rs-M_1, the second twice as wide as the first, from M_1 to anterior third of M_2-M_3, and the posterior bigger, about three times wider than the second, ovoid, from the posterior third in M_3-Cu_1 to the edge of Cu_2, all three with a white pupil at the centre and a broad and yellow external ring. A fourth minute black

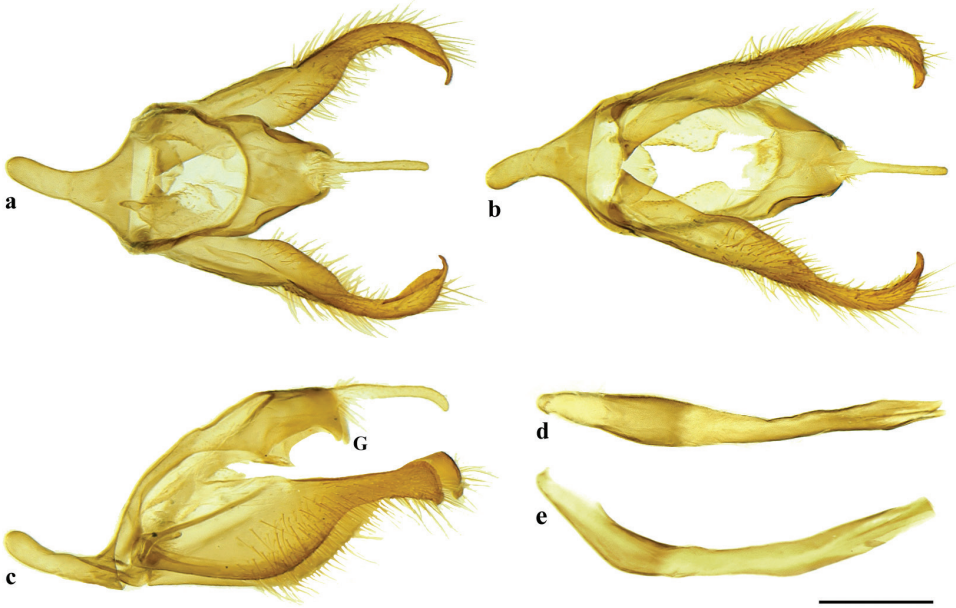


Figure 8. *Euptychia sophiae* sp. n. Genitalia of paratype male: **a** dorsal view **b** ventral view **c** lateral view ("G" indicates fused gnathos) **d** aedeagus, dorsal and **e** lateral views. DZUP collection. Photos by Diego R. Dolibaina. Scale bar: 0.5 mm.

ocellus, with a yellow outer ring but with no pupil, located on the anal margin at the base of the postmedian brown band. Marginal dark brown, thin, and crenulated line from $Sc+R_1$ to 3A. Fringes dark brown.

Male genitalia (Fig. 8). Tegumen dorsally flattened, trapezoidal, lateral posterior margin projecting ventrad as a short gnathos fused to the tegumen, subtriangular, nearly at right angle to uncus; uncus basally hairy, almost 10 times longer than wide, laterally apex curved downward; ventral arms of tegumen fused to anterior margin of tegumen; appendices angulares absent; anterior projection of saccus almost same length as uncus, dorsal arms of saccus combined with ventral arms from tegumen; valva sparsely hairy, basal two-thirds shaped vaguely as an elongated semi-circle, distal one-third rather narrow then widening to form a spatulate apex, distal half of valva in dorso-ventral view resembles propodus of a lobster (Decapoda: Nephropidae), but without the dactylus; aedeagus strongly curved upwards in lateral view, almost same length as valva, posterior portion opens latero-ventrally; cornuti absent.

FEMALE: Unknown.

Etymology. The specific epithet honours T. Zacca's niece, Laura Sophia. To prevent any future ambiguity, the name *sophiae* is considered to be a Latinised modern female noun in the genitive case.

Distribution and habitat. This species is only known from the type locality in Serra do Divisor National Park (SDNP), Acre, in the extreme west of Brazil, and from

Figure 9. View from the Instituto Chico Mendes (ICMBio) research station at 200 m elevation of the river Moa and lowland tropical rainforest on the flatlands and mountain slopes of the northern Serra do Divisor National Park. Photo by Diego R. Dolibaina.

Figure 10. Seasonally inundated lowland tropical rainforest habitat with a predominance of *Mauritia* palms (Arecaceae) in the northern Serra do Divisor National Park. Photo by Diego R. Dolibaina.

across the border in the neighbouring department of Loreto, in north-eastern Peru. The Brazilian specimens of *E. sophiae* were collected in forest characterized as submontane dense ombrophilous forest in a landscape of "terra firme" forest with patches of seasonally inundated areas with a predominance of palms in the genus *Mauritia* Linnaeus f. (Arecaceae) at about 200 m a.s.l. (see Figs 9, 10). A small north-south mountain range surrounds the low area in the western portion of the SDNP, with some hills as high as 600 m a.s.l. Only one hilltop was sampled (visible in Fig. 9) but no specimen of *E. sophiae* was collected there, although other species of *Euptychia* were observed. Despite subsequent expeditions in June 2013 and August 2014 to the same area of the SDNP, with five and seven collectors respectively, we were unable to find additional specimens of *E. sophiae*. Unfortunately, no behavioural notes were taken for this new species, but the three specimens known to us indicate a correlation with periods of average to below average rainfall, an observation similar to that made for *E. attenboroughi*. Only future sampling will indicate whether these two species show a distinct preference for avoiding the months of highest annual precipitation.

Host plant. Unknown.

Discussion

Males of *E. attenboroughi* and *E. sophiae*, especially *E. attenboroughi*, exhibit external wing pattern elements and wing morphology that are atypical for the genus, superficially recalling certain species in the genus *Chloreuptychia*. It was therefore important to support our generic classification for these two new taxa using more objective genetic analyses. Both new species are described in this genus on the basis of ML and Bayesian analyses of *E. sophiae*, reinforced by the ML analysis performed in Nakahara et al. (2015): all analyses suggest that *E. sophiae* should be a member of the monophyletic *Euptychia* clade with high support. Due to many external morphological similarities, including wing pattern and absence of a posterior projection of the tegumen in male genitalia, it is reasonable to consider *E. sophiae* to be a sister species of *E. attenboroughi*, which should therefore also be placed in *Euptychia*. The results indicate that the posterior projection of the tegumen is not shared by all members of the *Euptychia* clade, and that the absence of this character in these two species could be the result of secondary loss. Morphological evidence to support these two species in the *Euptychia* clade are: 1) presence of the forewing recurrent vein in the discal cell; 2) absence of basal swelling of the forewing cubital vein; 3) a relatively reduced humeral vein; 4) a developed 8th tergite and sternite in the male abdomen; 5) presence of the sclerotized region of the 8th abdominal segment in the female, located at the very basal side of the 8th abdominal segment; 6) absence of the lateral sclerotisation of the 8th abdominal segment of the female; 7) origin of the ductus seminalis at the posterior end of the ductus bursae; 8) absence of tibial spurs on the midleg and hindleg. States 1–7 are shared by all *Euptychia* species examined so far, and are rarely seen in other euptychiine butterflies. State 8 is shared by most species of *Euptychia* and those species that possess tibial spurs require

further investigation regarding their classification. It is also noteworthy that within Euptychiina those *Euptychia* species whose early stage biology is known have both unique hostplants and larval characters (DeVries 1987, Beccaloni et al. 2008): known hostplants are non-seed plants in Selaginellaceae (Lycopodiophyta) and Neckeraceae (Bryophyta). States 1-8, hostplants, and early stage characters are possible apomorphic characters for *Euptychia*. Further in-depth study of euptychiine butterflies will hopefully determine this.

Acknowledgements

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Systematics of Nothopsini (Serpentes, Dipsadidae), with a new species of *Synophis* from the Pacific Andean slopes of southwestern Ecuador

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Abstract

Within Dipsadinae, some recent authors have recognized a tribe Nothopsini containing the genera *Diaphorolepis*, *Emmochliophis*, *Nothopsis*, *Synophis*, and *Xenopholis*, on the basis of a number of putative morphological synapomorphies. However, molecular results suggest that *Nothopsis*, *Synophis*, and *Xenopholis* do not form a monophyletic group, while the remaining taxa are unsampled in recent molecular phylogenies. Here, DNA-sequence data for some *Diaphorolepis* and *Synophis* species are provided for the first time, as well as additional new sequences for *Nothopsis* and some *Synophis* species. Including these and other existing data for nothopsine species, previous studies showing that Nothopsini is not a natural group are corroborated. Nothopsini Cope, 1871 is restricted to *Nothopsis*. Diaphorolepidini Jenner, 1981 is resurrected and re-delimited to include only *Diaphorolepis*, *Emmochliophis*, and *Synophis*. Finally, *Xenopholis* remains Dipsadinae *incertae sedis.* Known material of Diaphorolepidini is reviewed to generate revised and expanded descriptions and diagnoses at the tribe, genus, and species level. Numerous cryptic species are likely present in *S. bicolor* and *S. lasallei*. Finally, a new population from the low-elevation cloud forests of SW Ecuador is reported upon, which is genetically and morphologically distinct from all other species, that is here named *Synophis zaheri* **sp. n.**

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Keywords
Serpentes, Dipsadinae, Nothopsini, *Diaphorolepis*, *Synophis*

Introduction

Within Dipsadinae (*sensu* Pyron et al. 2013), *Diaphorolepis*, *Emmochliophis*, *Nothopsis*, *Synophis*, and *Xenopholis* were historically thought to form a monophyletic group on the basis of scutellation, osteological, histological, hemipenial, and respiratory characters (see Sheil & Grant 2001). The group has been referred to as tribe Nothopsini by some authors (Savitzky 1974; Dowling and Duellman 1978). The genera *Amastridium*, *Chersodromus*, and *Ninia* have also been referred to this assemblage (Wallach 1995). Alternatively, Jenner (1981) proposed a tribe Diaphorolepidini containing *Diaphorolepis* along with *Atractus*, *Chersodromus*, *Crisantophis*, *Elapomorphus*, *Enulius*, *Gomesophis*, *Pseudotomodon*, *Ptychophis*, and *Sordellina*, while *Synophis* was placed in Philodryadini, and *Emmochliophis* was not accounted for.

Most subsequent studies have considered Nothopsini to contain only *Diaphorolepis*, *Emmochliophis*, *Nothopsis*, *Synophis*, and *Xenopholis* (see Sheil and Grant 2001; Martinez 2011). Some of these taxa, *Nothopsis* in particular, bear a strong external resemblance to Asian xenodermatids such as *Xenodermus* (Bogert 1964). In contrast, molecular phylogenetic analyses have strongly supported *Nothopsis* (Vidal et al. 2010), *Synophis* (Sheehy 2012), and *Xenopholis* (Vidal et al. 2010; Pyron et al. 2011; Grazziotin et al. 2012) as dipsadines, as does hemipenial morphology (Zaher 1999). However, these genera do not form a monophyletic group within Dipsadinae in molecular phylogenies, and are widely separated in different dipsadine clades (Vidal et al. 2010; Grazziotin et al. 2012; Sheehy 2012; Pyron et al. 2013).

Thus, the tribe Nothopsini does not appear to represent a natural group, despite the putative morphological synapomorphies uniting the taxa listed above (Savitzky 1974; Ferrarezzi 1994; Wallach 1995; Martinez 2011). Contrastingly, the strength of the molecular results suggests that these likely represent convergence, at least between *Nothopsis* and *Xenopholis*. This is not surprising, given the massive ecomorphological diversification exhibited by Dipsadinae following their adaptive radiation in the Neotropics (Cadle 1984a, b, c).

However, *Diaphorolepis* and *Emmochliophis* have still not been sampled in any molecular phylogeny, and it is thus unclear where their phylogenetic affinities lie. Morphological evidence suggests that these two genera form a clade with *Synophis* (see Hillis 1990). Furthermore, there are multiple species of *Synophis*, with potentially unclear species boundaries (Bogert 1964; Fritts and Smith 1969; Sheil 1998; Sheil and Grant 2001). Here, we report on new material from *Diaphorolepis*, *Synophis*, and *Nothopsis*, present a new molecular phylogeny, and describe a new species of *Synophis.* We review current knowledge of *Diaphorolepis*, *Emmochliophis*, and *Synophis*, and discuss species limits in these genera. Dipsadine diversity in the Andes is clearly underestimated, and new species are still being discovered in the 21st century (e.g., Salazar-Venezuela et al. 2014; Sheehy et al. 2014; Zaher et al. 2014).

Materials

Molecular phylogeny

Work in Ecuador was carried out under permit number MAE-DNB-CM-2015-0017. We obtained tissue samples of *Diaphorolepis wagneri* (3 specimens), *Synophis bicolor* (3), *S. calamitus* (1), *S. lasallei* (1), a new *Synophis* species (2), and *Nothopsis rugosus* (1), via fieldwork in Ecuador. The specimens are deposited at the Museo de Zoología at the Universidad Tecnológica Indoamérica (MZUTI; Tables 1, 2). We also obtained a tissue loan of the holotype of *S. calamitus* from Ecuador (KU 197107; Hillis 1990) from the University of Texas at Austin.

We isolated total DNA from liver tissue or tail tips by proteinase K digestion in lysis buffer, followed by protein precipitation with guanidine thiocyanate solution and final DNA precipitation using isopropyl alcohol. We used the following pairs of primers to amplify and sequence four mitochondrial genes (12S, 16S, CYTB, ND4) and one nuclear locus (CMOS): Snake_12S_F (5'-AAACTGGGATTAGATACCCCACTAT-3'), Snake_12S_R (5'-GTRCGCTTACCWTGTTACGACT-3'), Snake_16S_F (5'-CGCCTGTTTAYCAAAAACAT-3'), and Snake_16S_R (5'-CCGGTCTGAACTCAGATCACGT-3') from Kessing et al. (1989); Snake_Cytb_F (5'-GACCTGTGATMTGAAAACCAYCGTTGT-3') and Snake_Cytb_R (5'-CTTTGGTTTACAAGAACAATGCTTTA-3') from Burbrink et al. (2000); Snake_ND4_F (5'-CACCTATGACTACCAAAAGCTCATGTAGAAGC-3') and Snake_ND4_R (5'-CATTACTTTTACTTGGATTTGCACCA-3') from Arévalo et al. (1994); and Snake_cmosFs77 (5'-CATGGACTGGGATCAGTTATG-3') and Snake_cmosRs78 (5'-CCTTGGGTGTGATTTTCTCACCT-3') from Lawson et al. (2005).

We set up PCR reactions to a total volume of 25 µL containing MgCl2 2–3 mM , dNTPs 200 µM, 0.2 µM of each primer (0.8 µM in the case of ND4) and 1.25 U (16S and Cytb) or 0.625 U (ND4 and c-mos) of Taq DNA polymerase (Invitrogen). Thermocycling parameters consisted of an initial three-minute step at 94 °C; 25 to 30 cycles of 45–60 sec at 94 °C, 45 (16S and c-mos) or 60 (ND4 and Cytb) sec at 53–60 °C, 1 (16S and c-mos) or 2 (ND4 and Cytb) min at 72 °C; and a final extension of 7 min at 72 °C. We used 1.5% agarose gels to visualize the PCR products and QIAquick PCR purification Kit (QIAGEN) to remove unincorporated primers and dNTPs from every PCR reaction before they were sent to Macrogen Inc. for sequencing.

We combined these new data with the publically available sequences for *Nothopsis* and *Xenopholis* (Vidal et al. 2010; Grazziotin et al. 2012). We obtained additional sequences of *S. bicolor* from the Museu de Zoologia da Universidade de São Paulo (MHUA 14577 [Museo de Herpetología de la Universidad de Antioquia], from Colombia: 12S, 16S, CYTB, and CMOS) and the University of Texas, Arlington (UTA-R 55956 from Ecuador: CYTB and ND4).

We then included all publically available dipsadine species sampled for these genes. This matrix contains 24% missing data ('-'), but these have been shown not to have deleterious effects on taxon placement and support in previous analyses (e.g., Pyron

Table 1. Morphometric data for specimens of Diaphorolepidini species examined or from literature. Codes are: MT=maxillary teeth; IL=infralabials; SL=supralabials; PO=postoculars; V=ventrals; SC=subcaudals; D1-3=dorsal scale rows at neck, midbody, and vent; SVL=snout-vent length (mm); TL=tail length (mm). Museum codes are given in Sabaj-Perez (2013). Includes data from ReptiliaWebEcuador (Torres-Carvajal et al. 2014).

Species	Collection	MT	IL	SL	PO	V	SC	D1	D2	D3	SVL	TL	Sex
Diaphorolepis laevis	NMW 14860	16	10	8/9	2	157	84	19	19	17	350	145	-
Diaphorolepis wagneri	AMNH 49179	23	10	8	3	194	138	21	19	17	290	153	M
Diaphorolepis wagneri	GML 4-00014	25	10	9	2	197	133	21	19	17	355	187	F
Diaphorolepis wagneri	KU 75682	24	10	9	2	196	136	21	19	17	311	142	F
Diaphorolepis wagneri	MECN 2937	-	-	9	3	181	133	19	19	17	276	129	M
Diaphorolepis wagneri	MZUTI 3322	-	11	8	2	189	141	19	19	17	332	167	F
Diaphorolepis wagneri	MZUTI 3752	-	11	8	1	189	134	21	19	17	447	257	M
Diaphorolepis wagneri	MZUTI 3901	-	13	9	3	195	131	19	19	17	524	259	F
Diaphorolepis wagneri	NMW 18915	-	13	9	2	191	137	21	19	17	307	146	M
Diaphorolepis wagneri	ZSM 2708/0	25	12	9	2	193	98	21	19	17	484	200	F
Emmochliophis fugleri	UIMNH 78795	16	8	8	2	140	97	19	19	19	-	-	M
Emmochliophis miops	BMNH 1946.1.12.30	13	8	8	1	145	93	19	19	19	251	134	F
Eastern Andes													
Synophis aff. *bicolor*	FHGO 9186	-	11	9	2	164	105	19	17	17	379	184	M
Synophis aff. *bicolor*	MZUTI 3529	-	11	8	2	163	106	19	19	17	407	202	M
Synophis aff. *bicolor*	MZUTI 4180	-	11	9	2	152	100	19	19	18	457	214	M
Synophis aff. *bicolor*	UMMZ 91550	24/27	11	9	2	160	103	-	19	17	529	235	F
Synophis aff. *bicolor*	UMMZ 91551	-	-	8	2	161	105	-	19	17	535	230	F
Synophis aff. *bicolor*	UMMZ 91552	-	-	8	2	166	106	-	19	17	153	61	F
Western Andes													
Synophis aff. *bicolor*	BMNH 1940.2.30.31	-	-	8	2	162	118	21	19	17	408	241	M
Synophis aff. *bicolor*	CAS 23612	-	-	8	2	166	100	-	19	17	186	80	F
Synophis aff. *bicolor*	MCZ R-164530	-	11	9	2	164	116	-	19	17	367	208	-
Synophis aff. *bicolor*	QCAZ 10453	-	11	8	2	-	-	-	-	-	-	-	-
Synophis aff. *bicolor*	TCWC 66209	-	11	8	2	160	96	21	19	17	-	-	-
Synophis aff. *bicolor*	UMMZ 185812	-	10	8	2	165	105	-	19	17	144	66	-
Synophis aff. *bicolor*	UMMZ 185813	-	10	8	2	162	122	-	-	-	257	147	-
Synophis cf. *bicolor*	MHUA 14133	>23	12	8	2	193	127	-	19	-	-	-	M
Synophis cf. *bicolor*	MHUA 14577	24	11	8	2	190	131	19	19	17	-	-	-
Synophis cf. *bicolor*	MLS2072	-	11/10	8	2	184	127	-	19	17	407	210	M
Synophis bicolor	MECN 6732	-	9	8	2	174	138	19	17	17	361	236	M
Synophis bicolor	MECN 6733	-	9	8	2	174	132	19	19	17	406	245	M
Synophis bicolor	MECN 8076	-	9	8	2	183	135	19	17	17	376	233	M
Synophis bicolor	MZUT 257	16	9	8	2	180	136	-	19	17	-	-	-
Synophis bicolor	MZUTI 4175	-	11	8	2	174	143	19	19	17	365	245	M
Synophis bicolor	UTA R-55956	-	9	8	2	176	129	-	19	17	-	-	-
Synophis calamitus	KU 164208	-	9	8	1	163	125	21	19	17	142	73	-
Synophis calamitus	KU 197107	-	9	7	1	166	110	21	19	17	149	74	F
Synophis calamitus	MZUTI 3694	-	11	9	2	166	118	23	19	17	462	265	M
Synophis calamitus	QCAZ 11931	-	9	8	1	-	-	-	-	-	-	-	-

Species	Collection	MT	IL	SL	PO	V	SC	D1	D2	D3	SVL	TL	Sex
Synophis lasallei	FMNH 81313	24	-	-	2	154	112	-	21	-	292	158	F
Synophis lasallei	EPN S.974	-	-	-	2	156	116	-	21	-	175	90	M
Synophis lasallei	EPN S.975	24	-	-	2	155	119	-	21	-	354	201	M
Synophis lasallei	FHGO 6489	-	11	8	2	147	111	23	21	21	153	86	M
Synophis lasallei	FHGO 8340	-	11	8	2	153	88	21	19	17	415	199	M
Synophis lasallei	MCZ R-156873	-	11	7	1	147	115	-	-	-	412	206	-
Synophis lasallei	MECN 11250	-	10	8	2	153	98	21	19	17	412	196	F
Synophis lasallei	MECN 11262	-	-	8	2	154	118	21	21	17	306	145	M
Synophis lasallei	MECN 2220	-	10	8	2	165	117	19	19	17	294	146	M
Synophis lasallei	MLS/CJSP	-	-	-	2	144	101	-	-	-	300	170	M
Synophis lasallei	MZUTI 4181	-	11	9	2	156	29	21	21	19	272	42	M
Synophis lasallei	USNM 233061	-	11	9	2	156	124	-	21	-	285	160	M
Synophis lasallei	USNM 233062	-	11	8	2	153	126	-	22	20	360	200	-
Synophis lasallei	USNM 233063	-	11	8	2	151	86	23	21	19	308	197	M
Synophis lasallei	USNM 233064	-	11	8	2	151	-	-	21	19	270	150	-
Synophis plectovertebralis	UVC 11580	-	8	8	1	144	91	19	19	17	212	100	M
Synophis plectovertebralis	UVC 11858	-	7	7	1	147	79	19	19	17	196	76.5	F
Synophis zaheri	MZUTI 3353	-	8	8	2	166	112	19	19	17	351	184	M
Synophis zaheri	MZUTI 3355	-	9	8	2	169	111	19	19	17	372	194	M

et al. 2011). Data were aligned using MAFFT (Katoh and Standley 2013) under the default parameters in Geneious 7.1.9 (Biomatters Ltd.). We determined the optimal partitioning strategy using PartitionFinder (Lanfear et al. 2012). We estimated the phylogeny using MrBayes 3.2.5 (Ronquist et al. 2012), with 4 runs of 4 chains each, run for 20 million generations with the first 25% discarded as burnin. Convergence was assumed as the average standard deviation of split frequencies went to zero and the potential scale reduction factors went to one (Ronquist et al. 2012). The GenBank accession numbers for the new and existing data are given in Appendix I.

Morphological data

Species in *Diaphorolepis*, *Emmochliophis*, and *Synophis* have traditionally been delimited using easily determined external morphological characters (Bogert 1964; Hillis 1990). We relied here on a set of these characters, scored for museum specimens and our new material, to examine and delimit species boundaries (Table 1). For available specimens examined in person, in photographs, or in the literature, we recorded SVL and TL in mm, and counts of supralabials, infralabials, postoculars, ventrals, and subcaudals. We made cursory notes on the hemipenes of some male specimens when they were visible (Zaher 1999; Martinez 2011).

Results

Molecular phylogeny

The overall topology and support (Figs 1, 2) is similar to numerous recent studies (Zaher et al. 2009; Vidal et al. 2010; Pyron et al. 2011; Grazziotin et al. 2012). We consider strong support to be posterior probabilities ≥95%, following recent authors (Felsenstein 2004). Overall, there is low support for many backbone nodes, which may reflect inadequate sampling of taxa (only ~250 out of ~900 dipsadine species) or characters (only two independent loci).

Species in Dipsadinae can be broadly grouped into a primarily North American clade (*Contia* to *Carphophis* when viewing Fig. 1), a primarily Central American clade (*Diaphorolepis* to *Atractus* in Fig. 1), and a primarily South American clade (*Crisantophis* to *Apostolepis* in Fig. 2), though many species in the latter two clades range across both Central and South America. Several speciose genera in the primarily Central American clade are non-monophyletic, including *Imantodes*, *Hypsiglena*, *Geophis*, *Sibon*, *Dipsas*, *Sibynomorphus* (Fig. 1), as in previous studies (Grazziotin et al. 2012; Pyron et al. 2013).

In agreement with previous results (Grazziotin et al. 2012; Pyron et al. 2013), we find that Nothopsini is not a natural group (Fig. 1). The genus *Nothopsis* is strongly supported, and strongly placed with *Leptodeira* + *Imantodes* within the Central American clade. Correspondingly, *Xenopholis* is strongly supported and weakly nested within the South American clade, as the sister lineage to *Hydrodynastes*. It appears that one *Xenopholis scalaris* (KU 222204) from a previous study (Pyron et al. 2011) may have been misidentified, and is actually related to *X. undulatus*. This specimen is strongly supported as the sister lineage to the sampled *X. undulatus* (R-6955), to the exclusion of the three other sampled *X. scalaris*, which are strongly supported as a monophyletic group. This specimen is from the Peruvian Amazon and is pictured in Duellman and Mendelson (1995). The specimen pictured resembles the Amazonian *X. scalaris*, rather than the more xeric *X. undulatus* from the Brazilian shield. Thus, it is possible either that a curatorial or laboratory error occurred at some point, or that there is cryptic genetic diversity in *Xenopholis*.

A strongly-supported clade comprising *Diaphorolepis* and *Synophis* represents the sister to the large, primarily Central American clade that also contains *Nothopsis*. Monophyly of *Synophis* with respect to *Diaphorolepis* is weakly supported. Within a weakly paraphyletic *S. bicolor*, there are three deeply divergent lineages, and the sampled specimen of *S. lasallei*. An apparently new species of *Synophis* is the strongly-supported sister lineage of *S. calamitus*. The species *S. plectovertebralis* remains unsampled in the molecular phylogeny. Although *Emmochliophis* is not sampled, we follow previous authors in assuming a close relationship with *Diaphorolepis* and *Synophis*, given their strong resemblance (Savitzky 1974; Hillis 1990). Thus, the synapomorphies previously used to diagnose Nothopsini (Savitzky 1974; Wallach 1995) apparently represent convergence in at least three distantly related dipsadine lineages.

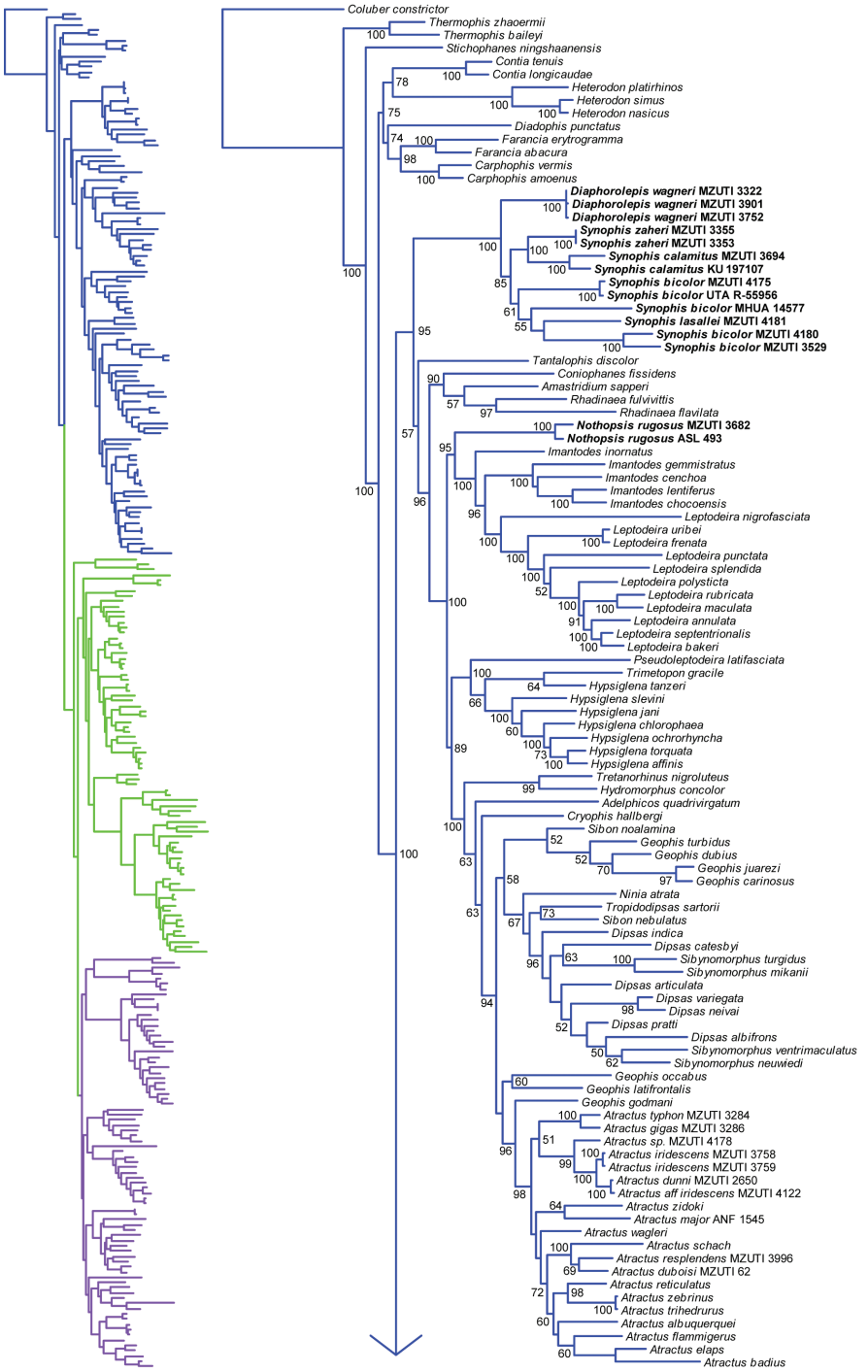

Figure 1. Phylogeny (part) of ~245 dipsadine species plus outgroups, based on partitioned, multi-gene Bayesian inference analysis of 3,462bp of mitochondrial and nuclear DNA. Support values given are posterior probabilities ≥50% from 15 million post-burnin generations.

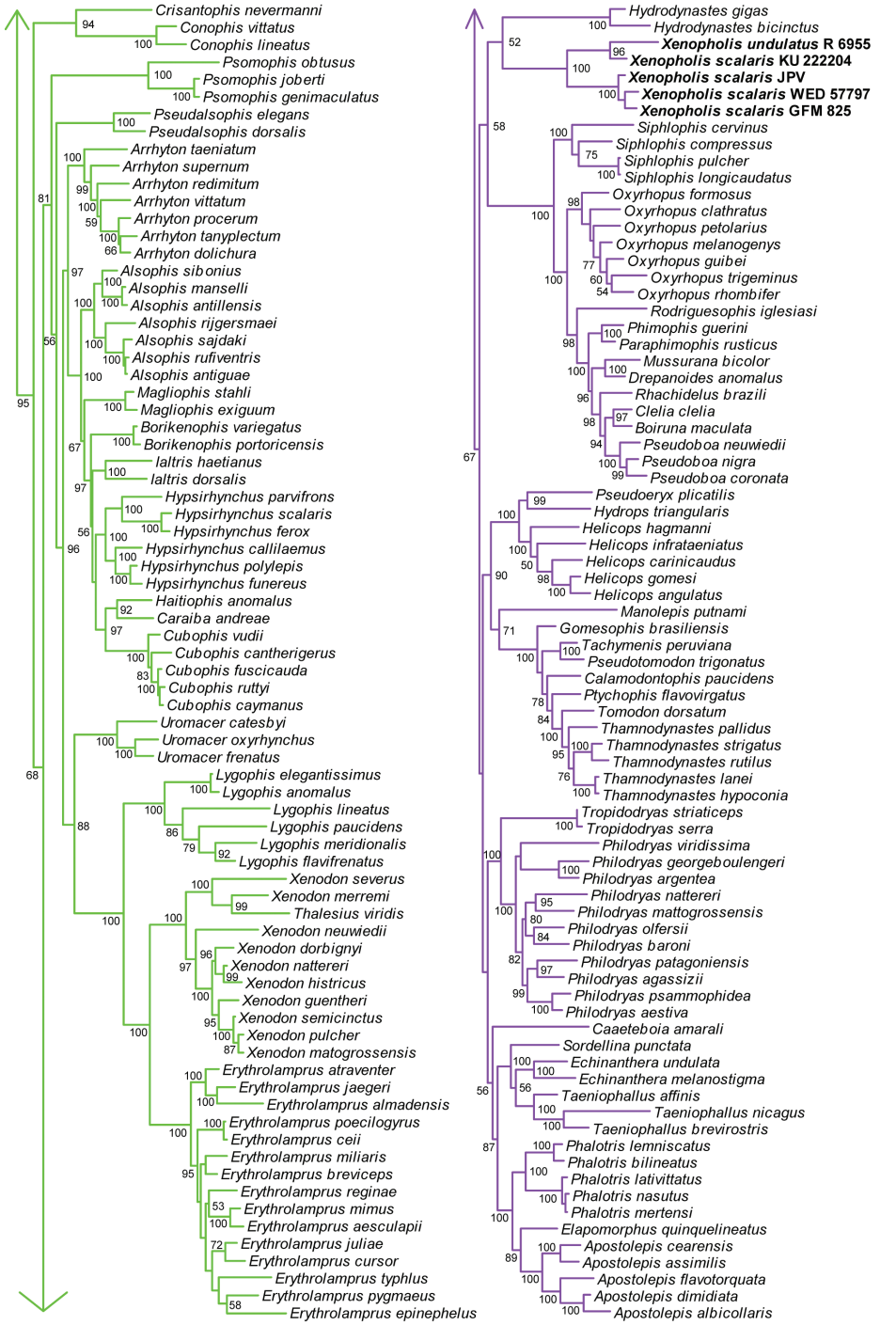

Figure 2. Phylogeny (part) of ~245 dipsadine species plus outgroups, based on partitioned, multi-gene Bayesian inference analysis of 3,462bp of mitochondrial and nuclear DNA. Support values given are posterior probabilities ≥50% from 15 million post-burnin generations.

Table 2. Vouchered localities for specimens of Diaphorolepidini species examined or from literature. In general, localities are given verbatim as transcribed from the literature, museum records, or field notes. Co-ordinates represent georeferencing attempts from gazetteers under standard guidelines, though some variation from the exact collecting locality will inevitably be present. Similarly, elevations are taken from Google Earth, and may not exactly match the elevations as originally reported. Museum codes are given in Sabaj-Perez (2013). Includes data from ReptiliaWebEcuador (Torres-Carvajal et al. 2014).

Species	Collection Number	Locality	Latitude	Longitude	Elev.
Diaphorolepis wagneri	GML 4-00014	Panama Darien, Cerro Mali, in Serrania del Darien	8.128557	-77.253498	1268
Diaphorolepis wagneri	MECN 2937	Canandé, Ecuador	0.529930	-79.035410	596
Diaphorolepis wagneri	MZUTI 3322	Milpe, Ecuador	0.034890	-78.867130	1076
Diaphorolepis wagneri	MZUTI 3901	Mashpi Lodge, Ecuador	0.164030	-78.870730	1068
Diaphorolepis wagneri	NMW 18915	El Palmar, Canar, Ecuador	-2.533300	-79.333300	325
Diaphorolepis wagneri	QCAZ 380	Ecuador, Cotopaxi, Las Pampas	-0.348360	-79.076010	1238
Diaphorolepis wagneri	QCAZ 381	Ecuador, Pichincha, Tandapi	-0.415220	-78.797280	1457
Diaphorolepis wagneri	QCAZ 8450	Ecuador, Cotopaxi, Pucayacu–Sigchos	-0.702730	-79.056810	974
Diaphorolepis wagneri	QCAZ 8782	Imbabura Lita, Ecuador	0.815270	-78.388350	865
Diaphorolepis wagneri	UVC 12187	18km East of San Jose de Palmar, Colombia	4.966667	-76.233333	1546
Diaphorolepis wagneri	UVC 5254	Colombia, Cali, Pichinde, Farallones de Cali	3.433400	-76.616680	1614
Diaphorolepis wagneri	UVC 5255	Colombia, Pance, Camino a Corea, Pance, Farallones de Cali	3.328340	-76.638650	1632
Emmochliophis fugleri	UIMNH 78795	4 km. E Río Baba Bridge, 24 km. S Santo Domingo de los Colorados, Pichincha, Ecuador	-0.435562	-79.246212	618
Emmochliophis miops	BMNH 1946.1.12.30	Parambas (Imbabura), Ecuador	0.805000	-78.350833	1105
Eastern Andes					
Synophis aff. *bicolor*	FHGO 9186	Río Zopladora, Ecuador	-2.611510	-78.472174	1677
Synophis aff. *bicolor*	KU 121341	Ecuador, Pastaza, Mera	-1.457452	-78.107976	1111
Synophis aff. *bicolor*	MZUTI 3529	Wild Sumaco, Ecuador	-0.675700	-77.601290	1463
Synophis aff. *bicolor*	MZUTI 4180	El Genairo, Ecuador	-4.166181	-78.94094	1212
Synophis aff. *bicolor*	UMMZ 91550	Ecuador, Napo-Pastaza, Abitagua	-1.383000	-78.083000	1482
Western Andes					
Synophis aff. *bicolor*	BMNH 1940.2.30.31	Río Solaya, Ecuador	-0.010213	-78.819510	1008
Synophis aff. *bicolor*	CAS 23612	Chimborazo, Naranjapata, Ecuador	-2.266667	-79.083333	763
Synophis aff. *bicolor*	MCZ R-164530	Ecuador, Pichincha, Tandapi	-0.419803	-78.801132	1714
Synophis aff. *bicolor*	QCAZ 10453	Cotopaxi: Naranjito, Bosque Integral Otonga	-0.417820	-78.988030	1655
Synophis aff. *bicolor*	TCWC 66209	Ecuador, Cotopaxi, Las Pampas	-0.348360	-79.076010	1238

Species	Collection Number	Locality	Latitude	Longitude	Elev.
Synophis aff. *bicolor*	UMMZ 185812	Ecuador, Cotopaxi, San Francisco de Las Pampas	-0.440357	-78.966629	1586
Synophis cf. *bicolor*	MHUA 14577	Colombia, Dpto. Antioquia, Mpio. Amalfi, V. da La Manguita, Fca. La Esperanza	6.978611	-75.044444	1394
Synophis cf. *bicolor*	MLS 2072	Medellin, Cordillera Central, Colombia	6.230833	-75.590556	1497
Synophis bicolor	MECN 6732	Tobar Donoso, Ecuador	1.189930	-78.504130	229
Synophis bicolor	MECN 6733	Sendero Awa, Ecuador	1.164400	-78.507120	257
Synophis bicolor	MZUTI 4175	Itapoa, Ecuador	0.46411	-79.15547	267
Synophis bicolor	UTA R-55956	Ecuador, Esmeraldas, Canton San Lorenzo	1.03212	-78.613780	318
Synophis calamitus	KU 164208	9 km SE Tandayapa, Pichincha Province, Ecuador	-0.047404	-78.632804	2169
Synophis calamitus	KU 197107	4 km SE Tandayapa, Pichincha Province, Ecuador	-0.012514	-78.650697	1889
Synophis calamitus	MZUTI 3694	Tambo Tanda, Ecuador	-0.020108	-78.651012	2048
Synophis lasallei	EPN S.974	Ecuador, Napo-Pastaza, nr. Río Talin, headwaters of the Río Bobonaza	-1.466670	-77.883300	948
Synophis lasallei	FHGO 6489	Ceploa, Ecuador	-1.339063	-77.670660	839
Synophis lasallei	FHGO 7770	Cara del Indio, Ecuador	-3.575695	-78.451020	1207
Synophis lasallei	FHGO 8340	El Quimi, Ecuador	-3.571852	-78.516598	752
Synophis lasallei	FMNH 81313	Colombia, Meta, Pico Renjifo, Serrania de la Macarena	2.476901	-73.794852	520
Synophis lasallei	KU 164221	2 km SSW Río Reventador, Ecuador	-0.100000	-77.600000	1479
Synophis lasallei	MCZ R-156873	Ecuador, Napo Prov., Inecel Station, Cascada San Rafael, Río Quijos	-0.103401	-77.585487	1290
Synophis lasallei	MECN 11250	Paquisha Alto, Ecuador	-3.909518	-78.487244	1660
Synophis lasallei	MECN 11262	El Pangui, Ecuador	-3.624502	-78.586510	814
Synophis lasallei	MECN 2220	Puyo, Ecuador	-1.466780	-77.983350	957
Synophis lasallei	MLS/CJSP	N of Alban, cen. Cundinamarca Dept., cen. Colombia	4.883333	-74.450000	1983
Synophis lasallei	MZUTI 4181	Sacha Yaku, Ecuador	-1.407882	-77.711092	974
Synophis lasallei	USNM 233061	Río Arajuno, headwaters of, tributary of Río Napo, Pastaza, Ecuador	-1.400000	-77.883300	969
Synophis lasallei	USNM 233062	Río Siquino, tributary of Río Villano, Upper Curaray, Pastaza, Ecuador	-1.455303	-77.714685	576
Synophis lasallei	USNM 233063	Río Bobonaza, headwaters of, Ecuador	-1.512156	-77.833454	594
Synophis lasallei	WWL 977-978	Colombia, Meta prov., Villavicencio	4.150000	-73.633333	539
Synophis plectovertebralis	UVC 11580	Haciendo San Pedro, 6km S El Queremal, Municipio Dagua, Valle del Cauca, Colombia	3.483333	-76.700000	1830
Synophis zaheri	MZUTI 3353	Buenaventura Lodge, Ecuador	-3.647970	-79.755070	874
Synophis zaheri	MZUTI 3355	Buenaventura Lodge, Ecuador	-3.648820	-79.756400	812

Systematics

We seek here to only name clades associated Nothopsini that are strongly supported in our molecular phylogeny. Above the genus level, Nothopsini is not a natural group in any of its recent conformations. We place *Nothopsis* alone in Nothopsini Cope, 1871. We resurrect and re-delimit the tribe Diaphorolepidini Jenner, 1981 to include only *Diaphorolepis*, *Emmochliophis*, and *Synophis.* The genus *Xenopholis* is not strongly supported in any supra-generic group and remains *incertae sedis* in Dipsadinae (see Grazziotin et al. 2012).

Our molecular and morphological data (Tables 1–3; Figs 1, 2) also corroborate previous authors in finding that genus and species boundaries within Diaphorolepidini are unclear and in need of revision (Sheil and Grant 2001). We here provide photographs and range maps of representative material (Figs 3–9). A number of issues are immediately apparent, and can be addressed with our results. We outline these below.

First, the head scalation of *Diaphorolepis wagneri* has not been accurately characterized by most authors (see Bogert 1964). Additionally, the holotype of *D. laevis* was incorrectly described with respect to several major characters (Werner 1923). Finally, reviewing museum specimens, including most holotypes, reveals that the current species boundaries and diagnoses are oftentimes inaccurate with respect to the observed range of variation in the relevant characters. In particular, the holotype of *S. bicolor* does not match many populations typically referred to this species (Bogert 1964; Hillis 1990; Sheil and Grant 2001).

In the case of *Diaphorolepis wagneri*, the postoculars can range from 1–3 (rather than 1–2), as illustrated by Bogert (1964), but not discussed explicitly. Werner (1901) apparently considered the small, lower postocular to be a subocular. Occasionally, the middle postocular will not be in contact with the brille, and resembles a temporal, behind the two remaining postoculars. As noted previously, the nasals are never divided, but only creased (Sheil and Grant 2001), contrary to reports from some previous authors (Bogert 1964; Hillis 1990).

In the case of *Diaphorolepis laevis*, Werner (1923) diagnosed the species as having fewer ventrals and subcaudals than *D. wagneri*, and smooth dorsal scales. Examination of the holotype (NMW 14860) reveals that it is indeed keeled, albeit weakly, throughout most of the midbody and posterior dorsal scale rows. This includes a bicarinate vertebral scale row that was previously considered to be diagnostic only of *D. wagneri.* The specimen appears to have a lighter-colored nuchal collar, though this may be a preservation artifact. The type locality within Colombia is unknown.

In the case of *Synophis bicolor*, the holotype (MZUT 257) has 180 ventrals, 136 subcaudals, and 9 infralabials, whereas sampled populations from the Andes of Ecuador typically have 152–166 ventrals, 96–122 subcaudals, and 10 or 11 infralabials. The locality of the holotype is unknown. Sampled populations from the Chocó of Ecuador match the holotype more closely, with 174–183 ventrals, 129–143 subcaudals, and 9–11 infralabials. The Chocóan populations typically occur at low to middle elevations (~200–300m), whereas Andean populations occur at higher elevations (~800–1700m).

Table 3. Summary of measured diagnostic characters (external meristic features) for diaphorolepidine species. These data are a summary of Table 1 (omitting some subcaudal scale counts from apparently truncated tails), and can be used to identify ambiguous specimens in the field or collections, and should be updated with new material in the future.

Species	MT	IL	SL	PO	V	SC	D1	D2	D3
Diaphorolepis laevis	16	10	8–9	2	157	84	19	19	17
Diaphorolepis wagneri	23–25	10–13	8–9	1–3	181–197	131–141	19–21	19	17
Emmochliophis fugleri	16	8	8	2	140	97	19	19	19
Emmochliophis miops	13	8	8	1	145	93	19	19	19
Synophis aff. *bicolor*	24–27	10–11	8–9	2	152–166	96–122	19–21	17–19	17–18
Synophis cf. *bicolor*	23–24	10–12	8	2	184–193	127–131	19	19	17
Synophis bicolor	16	9–11	8	2	174–183	129–143	19	17–19	17
Synophis calamitus	–	9–11	7–9	1–2	163–166	110–125	21–23	19	17
Synophis lasallei	24	10–11	7–9	1–2	144–165	101–126	19–23	19–22	17–21
Synophis plectovertebralis	–	7–8	7–8	1	144–147	79–91	19	19	17
Synophis zaheri	–	8–9	8	2	166–169	111–112	19	19	17

Populations from the northern western Andes of Colombia have 184–193 ventrals, 127–131 subcaudals, and 10–12 infralabials.

These three populations (Chocóan, Colombian Andean, and Ecuadorean Andean; Figs 3D, 4), correspond to three deeply divergent genetic lineages within *Synophis bicolor* (Fig. 1). A full revision of this species complex is pending further molecular and morphological sampling. We refer to the Chocóan populations as *S. bicolor*, the Ecuadorean Andean populations as *S.* aff. *bicolor*, and the Colombian Andean populations as *S.* cf. *bicolor* (using aff. versus cf. somewhat arbitrarily) for the remainder of the paper. The *S. bicolor* group is also weakly paraphyletic with respect to the sampled specimen of *S. lasallei*, which is the sister lineage of the Ecuadorean Andean lineages. The specimen of *S. lasallei* (MZUTI 4181) strongly matches the other *S. lasallei* specimens examined (Table 1), and is thus not a mis-identified *S. bicolor*.

Finally, we report here on two specimens of *Synophis* aff. *calamitus* from low to middle elevations on the Pacific versant of the Andes in SW Ecuador. These are diagnosable from the species above based on numerous characters, and we here name them:

***Synophis zaheri* sp. n.**
http://zoobank.org/
Figs 3, 5, 8

Holotype. MZUTI 3353 (Fig. 3A), an adult male collected on 30 December 2013 at ~2200h by Alejandro Arteaga, Lucas Bustamante, Rita Hidalgo, Daniel Mideros, and Diana Troya, in the vicinity of Buenaventura Reserve (Fundación Jocotoco), near Piñas, El Oro Province, SW Ecuador, 874m above sea level (-3.65, -79.76; Fig. 5), in a narrow band of cloud forest on the Pacific versant of the Andes.

Paratype. MZUTI 3355 (Fig. 3B), adult male collected a few minutes after the holotype, a few meters away.

Etymology. Named after the preeminent Brazilian herpetologist Hussam El-Dine Zaher, for his innumerable contributions to South American herpetology and snake systematics.

Diagnosis. *Synophis zaheri* can be differentiated from *Diaphorolepis* by an unmodified vertebral scale row with a single weak keel (versus a laterally expanded vertebral scale row, bicarinate or smooth); from *Emmochliophis* by the presence of a loreal (versus absence); from *S. bicolor* by having 166–169 ventrals (versus 174–183) and 111–112 subcaudals (versus 129–143); from *S.* aff. *bicolor* by having 8 or 9 infralabials (versus 10 or 11) and lighter brown dorsal coloration in life (versus darker black); from *S.* cf. *bicolor* by having 166–169 ventrals (versus 184–193), 111–112 subcaudals (versus 127–131), and 8 or 9 infralabials (versus 10–12); from *S. calamitus* by having two postoculars (versus one typically) and internasals in contact (versus divided typically); from *S. lasallei* by having 166–169 ventrals (versus 144–165), 19 dorsal scale rows at midbody (versus 21–23 typically), 8 or 9 infralabials (versus 10 or 11), and by having the anteriormost dorsal scale rows smooth (versus keeled); and from *S. plectrovertebralis* by absence of a nuchal collar (versus presence) and two postoculars (versus one).

Description. Small-sized snakes (351–372mm SVL, 184–194mm TL) with slender bodies and head distinct from neck. Eye large (>1/3 head height), bulbous, and black in life, with pupil not easily distinguishable from iris. Pupil round in preservative (though this may be an effect of fixation). Dorsum coloration grayish-brown with iridescent sheen in life and preservation, no light-colored nuchal collar in adults, and posterior supralabials mostly pigmented (>50%). Ventral coloration primarily bright yellowish-white, extending onto margins of ventral scales and supralabials. Posterior one-third of ventral surface anterior to vent becomes increasingly mottled, and ventral surface of tail color of dorsum. Squamation pattern includes 166–169 ventral scales, 111–112 subcaudals, 19-19-17 dorsal scale rows (scale-row reduction of 2 rows past midbody), anal single, no apical pits, mid-body dorsal scales with weak single keel (first few dorsal scale-rows smooth), vertebral scale row not enlarged, nuchal scales smooth, 8 supralabials, 8 or 9 infralabials, 2 postoculars, loreal present, nasal undivided, fused prefrontals, internasals in contact, and rostral concave. Condition of the vertebrae, which are heavily modified in *Emmochliophis* and *Synophis* (Fritts & Smith 1969; Savitzky 1974; Hillis 1990) unknown, pending skeletal preparation or micro-CT scanning. Everted hemipenes are slightly bilobed, semicalyculate, and semicapitate, relatively stout and bulbous, covered in large spines or hooks, similar to that of *Diaphorolepis* and *Synophis* aff. *bicolor* and *S. lasallei* (Bogert 1964; Zaher 1999; Martinez 2011). Both specimens were active by night in primary evergreen foothill forest, with canopy cover between 70 and 100%. The holotype MZUTI 3353 was found on the ground, whereas the paratype MZUTI 3355 was found 50 cm above the ground in a bush. Neither were found close to water, but were active after a rainy day.

In light of this new species and the updated material we have located and examined (Tables 1, 2), we have prepared updated accounts for the tribe and the other

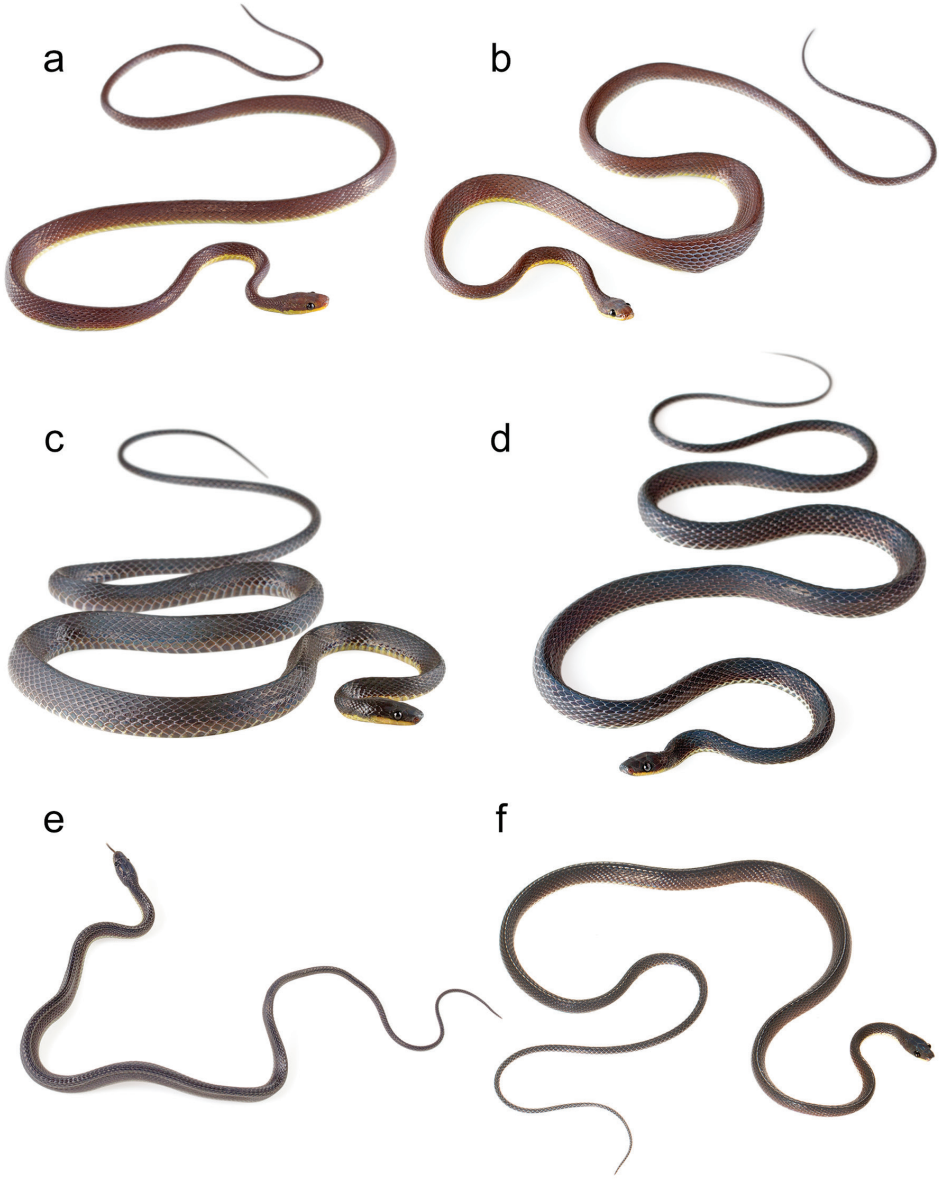

Figure 3. Photographs of some diaphorolepidine species in life: **a** *Synophis zaheri* MZUTI 3353 **b** *S. zaheri* MZUTI 3355 **c** *S. calamitus* MZUTI 3694 **d** *S.* aff. *bicolor* MZUTI 3529 **e** *S. lasallei* uncat., and **f** *Diaphorolepis wagneri* MZUTI 3901.

species. Hopefully, these will serve as useful descriptive summaries for taxonomic boundaries, species delimitation, and the assignment of new specimens and populations to species-level groups. We focus primarily on the external morphological characters that will be of greatest use for identifying specimens in the field and from

preserved collections. In some cases, more detailed information can be found in the original descriptions cited. The tribe name Diaphorolepidini was introduced in the PhD thesis of Jenner (1981), for which availability as a published work is ambiguous. We conservatively continue to credit the name to her, rather than treat it as unavailable and re-describe it ourselves.

Tribe Diaphorolepidini Jenner, 1981

Diaphorolepis Jan, 1863 (type genus by original designation)
Emmochliophis Fritts & Smith, 1969
Synophis Peracca, 1896

Etymology. Apparently from the Greek *diaphoros* for "differentiated" and *lepis* for "scales," likely referring to the enlarged vertebral scale row as compared to the rest of the dorsal scales.

Description. A group of relatively small-sized (<550mm SVL) dipsadine snakes restricted to the Darien of Panama and northern Andes of South America with fused prefrontals and either an expanded vertebral scale row (*Diaphorolepis*) or expanded zygapophyses and neural spines in adults (*Emmochliophis* and *Synophis*).

Notes. The tribe name has also been spelled 'Diaphorolepini' by Sheehy (2012), but Diaphorolepidini is the correct spelling based on the suffix *–lepis*, for which the stem is *–lepid* + *–ini*. This is a greatly restricted definition of Diaphorolepidini over the original description (Jenner 1981), which included *Atractus*, *Chersodromus*, *Crisantophis*, *Elapomorphus*, *Enulius*, *Gomesophis*, *Pseudotomodon*, *Ptychophis*, and *Sordellina*.

Genus *Diaphorolepis* Jan, 1863

Diaphorolepis laevis Werner, 1923
Diaphorolepis wagneri Jan, 1863 (type species by monotypy)

Etymology. Apparently from the Greek *diaphoros* for "differentiated" and *lepis* for "scales," likely referring to the enlarged vertebral scale row as compared to the rest of the dorsal scales.

Description. Relatively small-sized (<550mm SVL) dipsadine snakes restricted to the Darien in Panama and northern Andes of South America, with 16–25 maxillary teeth, 10–13 infralabials, 8 or 9 supralabials, fused prefrontals, internasals in contact, loreal present, 1–3 postoculars, 157–197 ventrals, 84–141 subcaudals, dorsal scales in (19–21)-19-17 rows, and expanded vertebral scale row with weak to strong double keeling.

Notes. This genus was validly described by Jan (1863), and re-described by Werner (1897). Werner (1901) later incorrectly deemed Jan's name a *nomen nudum*, and re-described the genus and type species, designating a neotype. However, this was an

error of interpretation, later realized by Werner himself (Werner 1929), and neither the re-description or neotype designation have any nomenclatural validity (see Bogert 1964). The lower subcaudal counts for some specimens likely represent truncated tails.

Diaphorolepis laevis Werner, 1923

Holotype. NMW 14860, locality given only as "Colombia."

Etymology. Apparently from the Latin *laevis* for "smooth," referring to the anterior dorsal scales.

Description. Relatively small-sized snake (350mm SVL) with 10 infralabials, 8/9 supralabials, 2 postoculars, internasals in contact, fused prefrontals, loreal present, nuchal collar apparently present, 16/18 maxillary teeth, 157 ventrals, 84 subcaudals, 19-19-17 dorsal scale rows, vertebral scale row is enlarged, with single keels on lateral dorsal scale rows and double keels on enlarged vertebral scale row weak to absent anteriorly and weak posteriorly. Uniformly light-colored venter and dark-colored dorsum in preservative. Nothing is known of the hemipenes or vertebrae.

Notes. Known only from the type specimen. The original description states that the dorsal scales are smooth, but weak keels are evident throughout the posterior portion of the body. A specimen at Harvard, reportedly from Leticia, Amazonas, Colombia, bears the identification *Diaphorolepis laevis* (MCZ R-143839). Upon examination, this specimen is clearly not *Diaphorolepis* on the basis of divided prefrontals (versus united in *Diaphorolepis*), lack of an enlarged bicarinate vertebral scale row (versus presence), and presence of an ocellated dorsal color-pattern (versus uniformly colored dorsum). The overall resemblance is of *Dipsas* sp.

Diaphorolepis wagneri Jan, 1863

Holotype. ZSM 2708/0, locality given only as "Andes of Ecuador." We revise this by subsequent restriction (*sensu* Smith 1953) to Milpé, Pichincha province, Ecuador (0.035, -78.87; 1076m), the locality of one of the specimens (MZUTI 3322) examined here.

Description. Relatively small-sized snakes (276–524mm SVL) with 23–25 maxillary teeth, 10–13 infralabials, 8 or 9 supralabials, 1–3 postoculars with the lower occasionally resembling a subocular and the middle occasionally resembling a temporal, fused prefrontals, internasals in contact, loreal present, incomplete nuchal collar present in juveniles (MZUTI 3322) fading ontogenetically, 181–197 ventrals, 131–141 subcaudals, (19–21)-19-17 dorsal scale rows, strong keels present on dorsal scales, and enlarged, bicarinate vertebral scale row. Uniformly cream-colored venter and dark-brown to black dorsum. Lumbar vertebrae are constricted near the middle, zygapophyses and neural spines are not expanded. The hemipenis has been briefly described (Bogert 1964), but prior to modern classifications of the organ

(Zaher 1999), and needs to be examined in more detail. Ranges at low to middle elevations (~300–1600m) along the Pacific versant from the Darien in Panama to central Ecuador.

Etymology. Most likely after Moritz Wagner, who collected the holotype (see Bauer 2013), and not Johann Andreas Wagner as suggested by previous authors (Beolens et al. 2011).

Notes. The re-description and neotype designation (NMW 18915) of Werner (1901) have no nomenclatural validity (see Bogert 1964).

Genus *Emmochliophis* Fritts & Smith, 1969

Emmochliophis fugleri Fritts & Smith, 1969 (type species by monotypy)
Emmochliophis miops (Boulenger, 1898)

Etymology. From the Greek *emmochlion* for "a socket for a bar" and *ophis* for "snake," referring to the unique interlocking vertebrae (Fritts and Smith 1969).

Description. Relatively small-sized (~250mm SVL) terrestrial snakes restricted to the Pacific Andean slopes of NW Ecuador, with a small number (<17) of maxillary teeth, 8 supralabials, 8 infralabials, fused prefrontals, internasals in contact, loreal absent, fewer than 150 ventrals, fewer than 100 subcaudals, dorsal scales in 19 rows without reduction, trunk vertebrae with lateral expansion of the zygapophyses, and expanded zygapophyses forming a rod-and-groove mechanism in *Emmochliophis fugleri*, but not in *E. miops*.

Notes. Both species are known only from the types. The hemipenis of *E. fugleri* has been briefly described (Fritts and Smith 1969), but prior to modern classifications of the organ (Zaher 1999), and needs to be examined in more detail. The organ is unknown in *E. miops*, as the sole known specimen is female (Sheil 1998).

Emmochliophis fugleri Fritts & Smith, 1969

Holotype. UIMNH 78795, 4 km. E Río Baba bridge, 24 km. S Santo Domingo de los Colorados, Pichincha, Ecuador, ~600 m.

Etymology. After Dr. Charles Fugler, who collected the holotype.

Description. A terrestrial snake from the Pacific Andean slopes of NW Ecuador, diagnosable by 16 maxillary teeth, 8 infralabials, 8 supralabials, 2 postoculars, internasals in contact, loreal absent, nuchal collar absent, 140 ventrals, 97 subcaudals, dorsal scales in 19 rows without reduction, strong keels, and zygapophyses expanded laterally forming rod–and–bar assembly. Type locality is surrounded by banana plantations. Little else is known about the habits or habitat of the species.

Notes. Known only from the type specimen, a male, collected by C. Fugler in February 1966.

Emmochliophis miops (Boulenger, 1898)

Synophis miops Boulenger, 1898

Holotype. BMNH 1946.1.12.30, Paramba, Ecuador (=Parambas, Imbabura *fide* Lynch and Duellman 1997)

Etymology. None given by Boulenger (1898); likely from the Greek *miops* for "myopia," in reference the species' small eyes, given as diagnostic by Boulenger.

Description. Relatively small-sized (~250mm SVL) terrestrial snake from the Pacific Andean slopes of NW Ecuador, diagnosable by 13 maxillary teeth, 8 infralabials, 8 supralabials, 1 postocular, internasals in contact, loreal absent, nuchal collar present, 145 ventrals, 93 subcaudals, dorsal scales in 19 rows without reduction, strong keels, and lateral expansion of the zygapophyses. Type locality is humid subtropical lower montane forest. Little else is known about the habits or habitat of the species. Stomach of type specimen contains remains of a gymnophthalmid lizard (Sheil 1998).

Notes. Known only from the type specimen, a female, collected by W. F. H. Rosenberg in October 1897. The type specimen was re-described in great detail by Sheil (1998).

Genus *Synophis* Peracca, 1896

Synophis bicolor Peracca, 1896 (type species by monotypy)
Synophis calamitus Hillis, 1990
Synophis lasallei (Nicéforo-Maria, 1950)
Synophis plectovertebralis Sheil & Grant, 2001
Synophis zaheri Pyron, Guayasamin, Peñafiel, Bustamante, & Arteaga, 2015

Etymology. None given by Peracca (1896); presumably from the Greek *syn-* for "with" or "together" and *ophis* for "snake," though the intended meaning of "with snake" is unclear.

Description. Relatively small-sized (~300mm SVL) dipsadine snakes of the Andes and Chocó of Colombia and Ecuador, with 16–27 maxillary teeth, 7–11 infralabials, 7–9 supralabials, fused prefrontals, loreal present, 1 or 2 postoculars, 144–184 ventrals, 88–138 subcaudals, dorsal scales in (19–21)-(17–21)-(17–20) rows, neural spine expanded and flattened, laterally expanded zygapophyses, and hemipenes slightly bilobed, semicalyculate, and semicapitate, relatively stout and bulbous, covered in large spines or hooks.

Notes. On the basis of similar scale counts, but apparently without examining specimens, Amaral (1929) considered the holotype of *Synophis bicolor* (at the time, the only known specimen from the only known species) to be synonymous with *Diaphorolepis wagneri*. These snakes are extremely rare, accounting for the paucity of knowledge and unclear species-boundaries. Numerous undescribed species from many new localities are known, and await description (*pers. comm.*, T. Grant, E. Meneses-Pelayo, O. Torres-Carvajal, and J. Arredondo).

Synophis bicolor Peracca, 1896

Holotype. MZUT 257, locality given only as "South America."

Etymology. None given by Peracca (1896); presumably from the Greek *bi-color* for "two colors," referring to the dark dorsum and light venter.

Description. Small-sized (~200–400mm SVL) dipsadine snakes of the Andes and Chocó of Colombia and Ecuador, diagnosable by 16–27 maxillary teeth, 9–12 infralabials, 8 or 9 supralabials, fused prefrontals, loreal present, 2 postoculars, 152–193 ventrals, 96–143 subcaudals, dorsal scales in (19–21)-(17–19)-(17–18) weakly keeled rows, neural spine expanded and flattened, laterally expanded zygapophyses, and hemipenes slightly bilobed, semicalyculate, and semicapitate, relatively stout and bulbous, covered in large spines or hooks. Populations of this species are found in both lowland Chocóan rainforest and Andean cloud forests. Individuals are often found in leaf litter or in bushes, active at night. One collection from the Pacific Andean slopes of Ecuador (UMMZ 185886–185891) represents clutches of 2, 2, and 8 eggs, with hatchlings 125–132mm SVL. Nothing is known of diet.

Notes. This is a species complex comprising at least three species-level taxa, which are distinct genetically, geographically, and morphologically (Figs 1, 3D, 4, 7, 9; Tables 1–3).

First are the Ecuadorean Andean highlands populations (*Synophis* aff. *bicolor*), which occur both on both the Pacific and Andean versants (~800–1700m). These are diagnosable by number of ventrals (152–166), subcaudals (96–122), infralabials (10 or 11), and supralabials (8 or 9), in combination. One individual (UMMZ 91550) has 24/27 maxillary teeth. The southernmost individual we examined (MZUTI 4180) has a very low number of ventral scales (152) compared to the remaining populations (160–166). Populations east and west of the Andes may also be a distinct species (O. Torres-Carvajal, *pers. comm.*), and are presented separately here. Most records from the Pacific versant north of the Río Toachi appear to represent *S. calamitus* (see below); one specimen reported from north of the river (BMNH 1940.2.30.31) may be mis-labeled, mis-identified, or the locality mis-referenced, or the species may be sympatric at some localities north of the river.

Second are the Chocóan populations from NW Ecuador, and presumably SW Colombia (~200–300m). These match the holotype in having 174–183 ventrals, 129–138 subcaudals, 8 supralabials, and typically 9 infralabials, though one specimen from further south (MZUTI 4175) has 11. We revise the type locality of *Synophis bicolor* by subsequent restriction (*sensu* Smith 1953) to Tobar Donoso, Carchi Province, Ecuador (1.19, -78.50), locality of several specimens examined here (Tables 1, 2; Figs 1, 4, 7, 9), to cement this association. Thus, this population represents *S. bicolor sensu stricto* in the case of future revision.

Third are the Colombian Andean highland populations (~1400–1500m; see Nicéforo-Maria 1970), which differ from the holotype in having 184–193 ventrals (versus 180), 127–131 subcaudals (versus 136), and 10–12 infralabials (versus 9). This group likely represents a third species, *Synophis* cf. *bicolor*. While we refrain from describing these additional *S. bicolor*-group species here based on limited current sampling, the

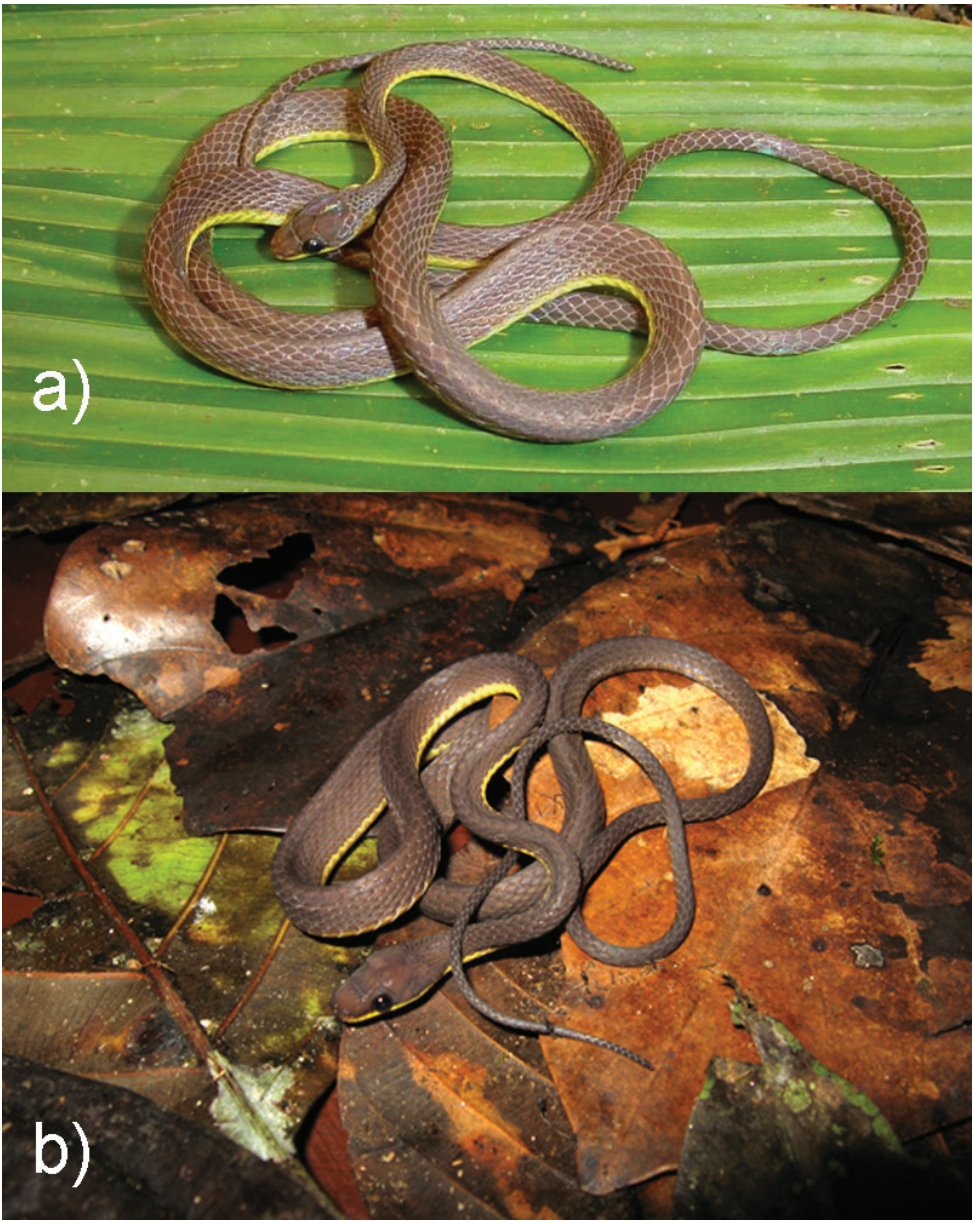

Figure 4. Photographs of some diaphorolepidine species in life: *Synophis bicolor* UTA R-55956 (**a**), and *S.* cf. *bicolor* MHUA 14577 (**b**).

populations described above likely represent at least two (Ecuadorean Andean highland and Colombian Andean Highland) if not three (E and W Ecuadorean and Colombian Andean highland) species.

Figure 5. Map of vouchered localities for *Synophis lasallei* (yellow circles), *S. plectovertebralis* (pink circles), *S. calamitus* (teal circles), *S. zaheri* (red circles), *Emmochliophis miops* (green triangle) and *E. fugleri* (blue triangle).

Synophis calamitus Hillis, 1990

Holotype. KU 197107, 4 km SE Tandayapa, Pichincha Province, Ecuador.

Paratype. KU 164208, 9km SE Tandayapa, Pichincha Province, Ecuador.

Etymology. From the Latin for "calamity," referring to accidents that befell the original collectors (Hillis 1990).

Figure 6. Map of vouchered localities for *Diaphorolepis wagneri* (teal squares).

Description. A group of relatively small (~450mm SVL) dipsadine snakes of the cloud forests of the Pacific versant of the Andean highlands of Ecuador diagnosable by 9–11 infralabials, 7–9 supralabials, fused prefrontals, internasals separated, loreal present, 1 or 2 postoculars, 163–166 ventrals, 110–125 subcaudals, dorsal scales in (21–23)-19-17 weakly keeled rows, neural spine expanded and flattened, and laterally expanded zygapophyses. Known from middle to high-elevation (~1900–2200m) cloud forests north of the Río Toachi. Nothing is known of diet or reproduction.

Figure 7. Map of vouchered localities for *Synophis bicolor* populations: *S. bicolor sensu stricto* (purple circles), western *S.* aff. *bicolor* (blue circles), eastern *S.* aff. *bicolor* (yellow circles), and *S.* cf. *bicolor* (teal circles).

Notes. A detailed description was also provided by Hillis (1990). The hemipenes have likely not been examined. Easily confused with *Synophis bicolor*; at least one specimen (QCAZ 11931) from near the type locality was originally mis-identified (O. Torres-Carvajal, *pers. comm.*). We suggest that all populations north of the Río Toachi are likely to represent *S. calamitus*. As mentioned above, one specimen apparently matching *S. bicolor* (BMNH 1940.2.30.31) is known from Río Soloya near Mindo north of Río Toachi, but this may have been mis-labeled, or mis-referenced

Figure 8. Photographs in preservation of some diaphorolepidine species. Upper: *Diaphorolepis wagneri* MZUTI 3901, Center: *Synophis zaheri* MZUTI 3355, Lower: *S. calamitus* MZUTI 3694.

geographically. The specimen of *"S. bicolor"* examined by Zaher (1999), QCAZ 452, cannot be located (O. Torres-Carvajal, *pers. comm.*), but originates from Chiriboga, Pichincha Province, Ecuador, north of Río Toachi, and thus may represent an *S. calamitus*. If this is the case, the hemipenes of *S. calamitus* and *S. lasallei* are nearly identical (Zaher 1999; Martinez 2011). Finally, one specimen sequenced here from Tambo Tanda (MZUTI 3694) appears to have aberrantly subdivided head scales, possessing

Figure 9. Photographs in preservation of some diaphorolepidine species. Upper: *Synophis bicolor* MZUTI 4175, Middle: *S. lasallei* MZUTI 4181, Lower: *S.* aff. *bicolor* MZUTI 4180.

one extra postocular, and 2 extra supralabials and infralabials (Fig. 8), which are misshapen and abnormally small. The badly damaged paratype also appears to have two postoculars on one side (O. Torres-Carvajal, *pers. comm.*). Thus, we concur with Hillis (1990) that one postocular, 7 or 8 supralabials, and 9 infralabials (along with the divided internasals and smooth anterior dorsal scale-rows) are generally diagnostic of the species, but with rare individual variation.

Synophis lasallei (Nicéforo-Maria, 1950)

Diaphorolepis lasallei Nicéforo-Maria, 1950

Holotype. MLS/CJSP uncat., from N of Albán, cen. Cundinamarca Dept., cen. Colombia.

Etymology. After the Instituto de La Salle, in Bogotá (Nicéforo-Maria 1950).

Description. Smaller (~300mm SVL) dipsadine snakes of the Amazonian versant of the Andes of Ecuador and Colombia, diagnosable by 24 maxillary teeth, 10 or 11 infralabials, 7–9 supralabials, fused prefrontals, internasals in contact, loreal present, 1 or 2 postoculars, nuchal collar absent, 144–165 ventrals, 101–126 subcaudals, dorsal scales in (19–23)-(19–22)-(17–21) strongly keeled rows even on head and neck, venter dark in some populations, neural spines expanded and flattened, and laterally expanded zygapophyses. Known from low to high elevations (~500–2000m) along the Amazonian versant of the Andes from central Colombia to central Ecuador. Nothing is known of diet or reproduction.

Notes. The hemipenes are very similar to both *Diaphorolepis* and *S. bicolor* (Bogert 1964; Zaher 1999; Martinez 2011). Much like *Synophis bicolor*, this species as currently described has a large geographic and elevational range, with wide variation in phenotype. There is significant variation in the number of dorsal scale rows and reduction thereof. One specimen from Ecuador (MCZ R-156873) has only one postocular and 7 supralabials, but otherwise matches the species. All other specimens have 2 and 8, respectively. Another specimen from Ecuador (MECN 2220) has 165 ventrals and 117 subcaudals with 19-19-17 scale rows, and is thus indistinguishable from *S.* aff. *bicolor*, with the exception of the strong keels on the nuchal scales and geographic distance from the nearest highland populations of *S.* aff. *bicolor*. All other specimens of *S. lasallei* have 144–156 ventrals, and most have (21–23)-(21–22)-(19–21) dorsal scale rows. Thus, it seems exceptionally likely that this is a species complex, possibly divided between highland and lowland, or northern and southern populations.

Synophis plectovertebralis Sheil & Grant, 2001

Holotype. UVC 11858, from Hacienda San Pedro, about 6 km south El Queremal, Municipio Dagua, Departamento del Valle del Cauca, Colombia.

Paratype. UVC 11580, from type locality.

Etymology. From the Latin *plecto-* for "braided" or "woven" and *veretbralis* for "vertebrae," referring to the appearance of the interlocking zygapophyses viewed from above (Sheil & Grant 2001).

Description. Relatively small (~200mm SVL) dipsadine snakes of the Pacific versant of the Andean Highlands of W Colombia, diagnosable by 24 maxillary teeth, 7 or 8 infralabials, 7 or 8 supralabials, fused prefrontals, internasals in contact, loreal present, 1 postocular, nuchal collar present, 144–147 ventrals, 79–91 subcaudals, dorsal scales in 19-19-17 weakly keeled rows, neural spines expanded and flattened, and later-

ally expanded zygapophyses forming a partially interlocking complex. The type locality is a middle elevation (~1800m) cloud forest. Both known specimens were collected in moist leaf litter; one was active at night. The stomach of the holotype contained a *Ptychoglossus stenolepis* (Sauria: Gymnophthalmidae).

Notes. Known only from the holotype and paratype (apparently juveniles), though other material has apparently been collected in Colombia, near the type locality (T. Grant and E. Meneses-Pelayo, *pers. comm.*). The hemipenes have not been examined. A more detailed description of the two specimens is provided by Sheil & Grant (2001).

Given our restriction of the name, we also provide the following re-description of the re-delimited Nothopsini. Note that we have not performed a comparative examination of a large series of preserved material, and these data are summarized from the literature (Dunn and Dowling 1957; Savage 2002; Kohler 2008; McCranie 2011) to provide a basis for future revisions.

Tribe Nothopsini Cope, 1871

Genus *Nothopsis* Cope, 1871 (type genus by monotypy)
Nothopsis rugosus Cope, 1871
Nothopsis affinis Boulenger, 1895 (Holotype BMNH 1946.1.15.62, "Salidero, NW Ecuador, 350ft") [subjective junior synonym of *N. rugosus fide* Dunn & Dowling 1957]
Nothopsis torresi Taylor, 1951 (Holotype KU 28710, "'Morehead' Finca, 5 miles southwest of Turrialba, Costa Rica") [subjective junior synonym of *N. rugosus fide* Dunn & Dowling 1957]

Holotype. USNM 12427, type locality "Isthmus of Darien [Panama]"

Etymology. From the Greek *nothos* for "bastard" and *opsis* for "appearance," with Cope (1871) apparently referring to putative mimicry of *Bothrops atrox*.

Description. A relatively small-sized (<350mm SVL) dipsadine snake, ranging in Central and South America from Honduras to Colombia and Ecuador, in lowland and middle-elevation rainforests, 250-900m, distinguishable from nearly all other similar or related snakes in the area by the rugose, granular nature of the dorsal scales, in particular lacking differentiation of the cephalic scales with the exception of well-defined internasals and poorly defined frontal and parietals, which are separated by rows of irregular, undifferentiated scales. Color pattern consists of irregular and poorly defined blotches of blackish or light, dark, and yellowish brown. With respect to the characters described here for diaphorolepidine species, *Nothopsis rugosus* typically exhibits 19–21 maxillary teeth, 9–13 supralabials, 11–16 infralabials, 149–162 ventrals, 81–112 subcaudals, dorsal scales in (24–30)-(26–30)-(22–26) rows, SVL of 151–320mm, and tail length of 61–133mm (see Dunn and Dowling 1957).

Notes. This taxon has historically been divided up into as many as three species (see Dunn and Dowling 1957), though only a single species is currently recognized. There may be cryptic variation or undiscovered diversity within this group. Note that

the family name was originally spelled Nothopidae by Cope (1871), but –*ops*– is the correct stem from –*opsis*, and Nothopsidae (and Nothopsini) is thus the correct spelling, as adopted by later authors.

Discussion

Systematics of Diaphorolepidini and Nothopsini

Corroborating previous results, we find that current supra-generic classification in Dipsadinae does not accurately reflect the phylogeny and describe natural groups in many cases (Pyron et al. 2011; Grazziotin et al. 2012). Support for monophyly and placement of many genera is low, and many other genera are apparently non-monophyletic. Efforts to clarify this situation are underway, sampling more taxa and characters (F. Grazziotin, *pers. comm.*). Only ~250 out of ~900 dipsadine species (Wallach et al. 2014) are sampled here for a few genes, but cryptic and undiscovered diversity is likely much higher in the group, and will require extensive additional sampling of taxa and characters to arrive at a stable phylogenetic and taxonomic resolution. The taxonomy of Dipsadinae has been contentious for quite some time (Cadle 1984a,b,c; Zaher 1999; Zaher et al. 2009; Grazziotin et al. 2012; Sheehy 2012), and will likely require extensive additional sampling of taxa and characters to provide a stable taxonomic resolution.

In particular, we find that Nothopsini is not monophyletic as historically defined, but that *Nothopsis* is strongly nested within a primarily Central American clade, with *Imantodes* and *Leptodeira*. We restrict tribe Nothopsini Cope, 1871 to *Nothopsis*. We resurrect and re-delimit Diaphorolepidini Jenner, 1981 to include only *Diaphorolepis*, *Emmochliophis*, and *Synophis*. Whereas *Emmochliophis* remains unsampled in the molecular phylogeny, it appears to be the sister-taxon of *Synophis* based on morphological data (Hillis, 1990). However, our phylogeny suggests that many of the morphological characters previously used to define supra-generic groups in Dipsadinae (see Savitzky 1974; Wallach 1995) are subject to strong and rapid convergence. Thus, future studies may find an alternative placement for this genus. Finally, the genus *Xenopholis* is weakly nested within a primarily South American clade, and remains Dipsadinae *incertae sedis*.

Species limits in Diaphorolepidini

Larger sample sizes reveal expanded ranges of diagnostic characters previously used to delimit species in Diaphorolepidini. These will hopefully assist future researchers in describing new taxa, and re-delimiting species boundaries. In particular, both *Synophis bicolor* and *S. lasallaei* may comprise multiple distinct species. Additional DNA sequencing and meristic and mensural measurements of more specimens should help clarify taxonomic boundaries.

In the case of *Synophis bicolor*, the Chocóan populations in Ecuador and presumably nearby Colombia match the description of the holotype, and thus likely represent the source of the original specimen, which remains to be re-described in detail. Contrastingly, highland populations in the Andean Highlands of Ecuador and Colombia are morphologically and genetically distinct, and both likely represent undescribed species. In the Ecuadorean Andes, populations of this taxon occur on both the Pacific and Amazonian versants, which may also be distinct from each other. The sampled specimen of *S. lasallei* is weakly nested within the sampled specimens of *S. bicolor*. A wide range of squamation and color pattern is observed in *S. lasallei*, which may represent cryptic species, as well as potential mis-identification of examined specimens. Finally, a cloud-forest population from the Pacific versant in SW Ecuador represents a new species described here as *S. zaheri*, allied to *S. calamitus*. Understanding the geographic distribution and genetic diversity in these taxa will require additional genetic sampling, which is hampered by the rarity of these species.

One of the most distinctive features of diaphorolepidine species is the highly modified condition of the vertebrae, in which the prezygapophyses and postzygapophyses are broadly expanded, forming ridges, and occasionally interlocking (Bogert 1964; Fritts and Smith 1969; Hillis 1990). Given the difficulty of preparing the skeletal material and the extreme rarity of specimens, this was not examined for *S. zaheri* or any additional specimens examined here. However, this may be a crucial character for future systematic revisions in the group, possibly utilizing micro-CT scanning or radiography.

Another possible source of information for delimiting species are the hemipenes. The organs are highly similar in *Diaphorolepis* and most *Synophis* species (Bogert 1964; Jenner 1981; Hillis 1990; Zaher 1999). Our observations agree with previous authors that the hemipenes are not strongly differentiated among species, though larger comparative series may reveal characters that serve to better diagnose species-level groups. In particular, the hemipenes are "nearly identical" in *S. bicolor* and *S. lasallei* (Zaher 1999; Martinez 2011), and our examination of *S. zaheri* shows no obvious qualitative differences. It is possible that speciation is primarily ecological or allopatric in this group, and thus there is little physical reproductive isolation.

Conclusions

Higher-level taxonomy in Dipsadinae is still partially unresolved, and many genera and supra-generic groups are either non-monophyletic, or poorly supported and weakly placed. This includes Nothopsini Cope, 1871, which must be restricted to *Nothopsis*, if it is used at all. We resurrect and re-delimit Diaphorolepidini Jenner, 1981 to include only *Diaphorolepis*, *Emmochliophis*, and *Synophis*. The genus *Xenopholis* remains Dipsadinae *incertae sedis.* Revised and expanded diagnoses in Diaphorolepidini support the distinctiveness of all currently recognized taxa. Cryptic species are likely present in *S. bicolor* and *S. lasallei*. A new population from the cloud forest of SW Ecuador is morphologically and genetically distinct, and we here name it *S. zaheri*. We hope that these

data will provide a robust platform for future researchers to examine species boundaries in Diaphorolepidini, as additional work clearly remains to be done. This is hampered, however, by the extreme rarity of these species.

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Appendix I

GenBank accession numbers for Dipsadinae and outgroup species analyzed here.

Species	12S	16S	CYTB	ND4	CMOS
Adelphicos quadrivirgatum	-	-	GQ895853	-	GQ895796
Alsophis antiguae	AF158455	AF158524	-	-	-
Alsophis antillensis	FJ416691	FJ416702	FJ416726	FJ416800	-
Alsophis manselli	-	AF158528	FJ416727	FJ416801	-
Alsophis rijgersmaei	FJ416697	FJ416708	FJ416729	FJ416803	-
Alsophis rufiventris	FJ416698	FJ416709	FJ416730	FJ416804	-
Alsophis sajdaki	-	-	FJ416731	FJ416805	-
Alsophis sibonius	FJ416692	FJ416703	FJ416728	FJ416802	-
Amastridium sapperi	-	-	GQ334479	GQ334580	-
Apostolepis albicollaris	JQ598793	JQ598856	-	-	JQ598965
Apostolepis assimilis	GQ457781	GQ457724	-	-	GQ457843
Apostolepis cearensis	JQ598794	JQ598857	-	-	JQ598966
Apostolepis dimidiata	GQ457782	GQ457725	JQ598917	-	GQ457844
Apostolepis flavotorquata	JQ598795	JQ598858	GQ895854	-	GQ895798
Arrhyton dolichura	AF158438	AF158507	FJ416721	FJ416795	-
Arrhyton procerum	AF158452	AF158521	FJ416723	FJ416797	-
Arrhyton redimitum	AF158439	AF158508	FJ416720	FJ416794	-
Arrhyton supernum	AF158436	AF158505	FJ416718	FJ416792	-
Arrhyton taeniatum	AF158453	AF158522	FJ416717	FJ416791	-
Arrhyton tanyplectum	AF158446	AF158516	FJ416722	FJ416796	-
Arrhyton vittatum	AF158437	AF158506	FJ416719	FJ416793	-
Atractus aff. *iridescens* MZUTI4122	-	KT944037	KT944049	KT944056	-
Atractus albuquerquei	GQ457783	GQ457726	JQ598918	-	GQ457845
Atractus badius	AF158425	AF158485	-	-	-
Atractus duboisi MZUTI62	-	KT944041	-	KT944059	-
Atractus dunni MZUTI2650	-	KT944038	KT944050	KT944057	-
Atractus elaps	-	-	EF078536	EF078584	-
Atractus flammigerus	AF158402	AF158471	-	-	-
Atractus gigas MZUTI3286	-	KT944043	KT944053	KT944061	-
Atractus iridescens MZUTI3758	-	-	KT944052	-	-
Atractus iridescens MZUTI3759	-	KT944039	KT944051	KT944058	-
Atractus major ANF1545	-	KT944045	-	-	-
Atractus resplendens MZUTI3996	KT944036	KT944042	KT944055	KT944060	-
Atractus reticulatus	JQ598798	JQ598886	-	-	JQ598970
Atractus schach	JQ598799	AF158486	-	-	JQ598971
Atractus sp. MZUTI4178	-	KT944040	-	-	KT944066
Atractus trihedrurus	GQ457784	GQ457727	JQ598919	-	GQ457846
Atractus typhon MZUTI3284	-	KT944044	KT944054	KT944062	-
Atractus wagleri	-	-	GQ334480	GQ334581	-
Atractus zebrinus	JQ598800	JQ598861	-	-	JQ598972
Atractus zidoki	AF158426	AF158487	-	-	-
Boiruna maculata	GQ457785	JQ598862	GQ895855	-	GQ895799

Species	**12S**	**16S**	**CYTB**	**ND4**	**CMOS**
Borikenophis portoricensis	FJ416696	AF158517	AF471085	U49308	AF471126
Borikenophis variegatus	FJ416700	FJ416711	FJ416734	FJ416808	-
Caaeteboia amarali	GQ457807	GQ457747	JQ598921	-	GQ457867
Calamodontophis paucidens	GQ457786	GQ457728	-	-	GQ457848
Caraiba andreae	AF158442	AF158511	FJ416743	FJ416817	-
Carphophis amoenus	AY577013	AY577022	AF471067	-	DQ112082
Carphophis vermis	-	-	KP765656	-	-
Clelia clelia	AF158403	AF158472	-	-	JQ598973
Coluber constrictor	L01765	L01770	EU180432	AY487040	AY486937
Coniophanes fissidens	-	-	EF078538	EF078586	-
Conophis lineatus	GQ457788	JQ598865	JQ598924	-	JQ598975
Conophis vittatus	-	-	GQ895861	-	GQ895805
Contia longicaudae	-	-	GU112407	GU112427	-
Contia tenuis	AY577021	AY577030	GU112401	AF402658	AF471134
Crisantophis nevermanni	GU018152	GU018169	-	-	-
Cryophis hallbergi	-	-	GQ895863	EF078544	GQ895807
Cubophis cantherigerus	AF158405	AF158475	AF544669	FJ416818	AF544694
Cubophis caymanus	FJ416693	FJ416704	FJ416745	FJ416820	-
Cubophis fuscicauda	FJ416695	FJ416706	FJ416747	FJ416822	-
Cubophis ruttyi	FJ416699	FJ416710	FJ416746	FJ416821	-
Cubophis vudii	AF158443	AF158512	FJ416744	FJ416819	-
Diadophis punctatus	AF544765	AY577024	EU193700	EU193987	AF471122
Diaphorolepis wagneri MZUTI3322	-	KR814752	-	KR814775	KR814764
Diaphorolepis wagneri MZUTI3752	-	KR814753	-	KR814777	KR814766
Diaphorolepis wagneri MZUTI3901	-	KR814754	-	KR814778	KR814767
Dipsas albifrons	JQ598803	JQ598866	JQ598925	-	-
Dipsas articulata	JQ598804	JQ598867	-	-	-
Dipsas catesbyi	JQ598805	Z46496	JQ598926	EF078585	JQ598977
Dipsas indica	GQ457789	GQ457730	-	-	GQ457850
Dipsas neivai	GQ457790	GQ457731	-	-	GQ457851
Dipsas pratti	-	-	GQ334482	GQ334583	-
Dipsas variegata	AF158406	AF158476	-	-	-
Drepanoides anomalus	GQ457791	GQ457732	GQ895866	-	GQ895810
Echinanthera melanostigma	JQ598806	GU018174	JQ598928	-	-
Echinanthera undulata	JQ598807	JQ598870	JQ598929	-	JQ598978
Elapomorphus quinquelineatus	GQ457794	GQ457735	JQ598930	-	GQ457855
Erythrolamprus aesculapii	GQ457795	GQ457736	GQ895871	-	GQ895814
Erythrolamprus almadensis	JQ598808	JQ598871	-	-	JQ598979
Erythrolamprus atraventer	JQ598809	JQ598872	-	-	JQ598980
Erythrolamprus breviceps	AF158464	AF158533	-	-	-
Erythrolamprus ceii	JQ598810	JQ598873	-	-	JQ598981
Erythrolamprus cursor	JX905310	JX905314	-	-	-
Erythrolamprus epinephelus	GU018158	GU018176	-	-	-
Erythrolamprus jaegeri	GQ457809	GQ457749	-	-	GQ457869
Erythrolamprus juliae	AF158445	AF158514	-	-	-
Erythrolamprus miliaris	JQ598811	AF158480	JQ598931	-	JQ598982

Species	12S	16S	CYTB	ND4	CMOS
Erythrolamprus mimus	GU018157	GU018175	-	-	-
Erythrolamprus poecilogyrus	JQ598812	JQ598875	-	-	-
Erythrolamprus pygmaeus	GU018154	GU018172	-	-	-
Erythrolamprus reginae	JQ598813	JQ598876	-	-	JQ598983
Erythrolamprus typhlus	GQ457811	GQ457751	-	-	GQ457871
Farancia abacura	Z46467	Z46491	U69832	DQ902307	AF471141
Farancia erytrogramma	AY577017	AY577026	KP765663	-	-
Geophis carinosus	-	-	GQ895872	-	GQ895815
Geophis dubius	-	-	KC917319	-	-
Geophis godmani	JQ598814	JQ598877	JQ598932	-	-
Geophis juarezi	-	-	KC917315	-	-
Geophis latifrontalis	-	-	KC917322	-	-
Geophis occabus	-	-	KC917323	-	-
Geophis turbidus	-	-	KC917321	-	-
Gomesophis brasiliensis	GQ457796	GQ457737	-	-	-
Haitiophis anomalus	FJ666091	FJ666092	-	-	-
Helicops angulatus	GQ457797	GQ457738	AF471037	-	AF471160
Helicops carinicaudus	JQ598815	-	-	-	JQ598984
Helicops gomesi	GQ457798	GQ457739	-	-	GQ457858
Helicops hagmanni	JQ598816	JQ598878	-	-	JQ598985
Helicops infrataeniatus	GQ457799	GQ457740	JQ598933	-	GQ457859
Heterodon nasicus	GQ457801	AY577027	KP765664	-	GQ457861
Heterodon platirhinos	AY577019	AY577028	GU112412	AF402659	JQ598986
Heterodon simus	AY577020	AY577029	AF217840	DQ902310	AF471142
Hydrodynastes bicinctus	GQ457802	GQ457742	JQ598935	-	GQ457862
Hydrodynastes gigas	GQ457803	GQ457743	GQ895873	-	GQ895816
Hydromorphus concolor	-	-	GQ895874	-	GQ895817
Hydrops triangularis	GQ457804	GQ457744	AF471039	-	AF471158
Hypsiglena affinis	-	-	GU353241	EU363055	-
Hypsiglena chlorophaea	EU728577	EU728577	EU728577	EU728577	-
Hypsiglena jani	EU728592	EU728592	EU728592	EU728592	-
Hypsiglena ochrorhyncha	EU728578	EU728578	EU728578	EU728578	-
Hypsiglena slevini	EU728584	EU728584	EU728584	EU728584	-
Hypsiglena tanzeri	-	-	EU728588	EU363044	-
Hypsiglena torquata	EU728591	EU728591	EU728591	EU728591	AF471159
Hypsirhynchus callilaemus	AF158440	AF158509	FJ416737	FJ416811	-
Hypsirhynchus ferox	AF158447	AF158515	GQ895875	FJ416816	GQ895818
Hypsirhynchus funereus	AF158451	AF158520	FJ416739	FJ416813	-
Hypsirhynchus parvifrons	AF158441	AF158510	FJ416740	FJ416814	-
Hypsirhynchus polylepis	AF158450	AF158519	FJ416738	FJ416812	-
Hypsirhynchus scalaris	AF158449	AF158518	FJ416741	FJ416815	-
Ialtris dorsalis	AF158456	AF158525	FJ416735	FJ416809	-
Ialtris haetianus	AF158458	AF158527	FJ416736	FJ416810	-
Imantodes cenchoa	EU728586	EU728586	EU728586	EU728586	GQ457865
Imantodes chocoensis	-	-	KC176250	-	-
Imantodes gemmistratus	-	-	GQ334487	EF078557	-

Species	12S	16S	CYTB	ND4	CMOS
Imantodes inornatus	-	-	GQ334489	EF078559	-
Imantodes lentiferus	AF158463	AF158532	KC176252	EF078561	-
Leptodeira annulata	GQ457806	GQ457746	FJ416713	FJ416787	AF544690
Leptodeira bakeri	-	-	GQ334518	GQ334618	-
Leptodeira frenata	-	-	EF078532	EF078580	-
Leptodeira maculata	-	-	GQ334524	GQ334623	-
Leptodeira nigrofasciata	-	-	GQ334526	EF078581	-
Leptodeira polysticta	EU728590	EU728590	EU728590	EU728590	-
Leptodeira punctata	-	-	EF078530	EF078577	-
Leptodeira rubricata	-	-	GQ334527	GQ334631	-
Leptodeira septentrionalis	GU018148	GU018163	KC176243	KC176255	-
Leptodeira splendida	-	-	EF078521	EF078569	-
Leptodeira uribei	-	-	EF078531	EF078579	-
Lygophis anomalus	JQ598817	JQ598879	-	-	-
Lygophis elegantissimus	GQ457808	GQ457748	-	-	GQ457868
Lygophis flavifrenatus	JQ598818	JQ598880	-	-	-
Lygophis lineatus	-	-	-	-	DQ469789
Lygophis meridionalis	GQ457810	GQ457750	-	-	GQ457870
Lygophis paucidens	JQ598819	-	-	-	JQ598987
Magliophis exiguum	FJ416694	AF158526	AF471071	FJ416798	AF471117
Magliophis stahli	-	-	FJ416725	FJ416799	-
Manolepis putnami	JQ598820	JQ598881	JQ598936	-	JQ598988
Mussurana bicolor	GQ457787	GQ457729	-	-	GQ457849
Ninia atrata	GQ457814	JQ598882	JQ598937	GQ334659	GQ457874
Nothopsis rugosus ASL493	GU018159	GU018177	-	-	-
Nothopsis rugosus MZUTI3682	-	KR814760	KR814770	KR814779	KR814768
Oxyrhopus clathratus	GQ457815	GQ457754	-	-	GQ457875
Oxyrhopus formosus	JQ598821	AF158482	-	-	-
Oxyrhopus guibei	JQ598822	JQ627291	JQ598938	-	JQ598989
Oxyrhopus melanogenys	JQ598823	AF158489	-	-	JQ598990
Oxyrhopus petolarius	GU018144	GU018170	GQ334554	GQ334660	-
Oxyrhopus rhombifer	GQ457816	GQ457755	-	-	GQ457876
Oxyrhopus trigeminus	JQ598824	JQ598884	JQ598939	-	-
Paraphimophis rusticus	JQ598802	JQ598864	JQ598923	-	JQ598974
Phalotris bilineatus	JQ598827	JQ598887	JQ598943	-	-
Phalotris lativittatus	JQ598825	JQ598885	-	-	JQ598991
Phalotris lemniscatus	GQ457817	GQ457756	JQ598941	-	GQ457877
Phalotris mertensi	JQ598826	-	-	-	-
Phalotris nasutus	GQ457818	GQ457757	GQ895880	-	GQ895822
Philodryas aestiva	GQ457819	GQ457758	-	-	GQ457879
Philodryas agassizii	GQ457823	GQ457762	GQ895883	-	GQ457883
Philodryas argentea	GQ457842	GQ457780	JQ598944	-	GQ457899
Philodryas baroni	JQ598828	JQ598888	-	-	-
Philodryas georgeboulengeri	-	-	GQ895898	-	GQ895838
Philodryas mattogrossensis	GQ457820	GQ457759	-	-	GQ457880
Philodryas nattereri	JQ598829	JQ598889	AF236806	-	JQ598992

Species	12S	16S	CYTB	ND4	CMOS
Philodryas olfersii	JQ598830	AF158484	JQ598945	-	JQ598993
Philodryas patagoniensis	GQ457821	JQ627296	AF236808	-	GQ457881
Philodryas psammophidea	GU018149	GU018168	-	-	-
Philodryas viridissima	AF158419	AF158474	AF236807	-	-
Phimophis guerini	GQ457822	GQ457761	-	-	GQ457882
Pseudalsophis dorsalis	JQ598832	JQ598892	JQ598946	-	JQ598994
Pseudalsophis elegans	AF158401	AF158470	JQ598947	-	JQ598995
Pseudoboa coronata	GQ457824	GQ457763	-	-	GQ457884
Pseudoboa neuwiedii	AF158423	AF158490	GQ895884	-	GQ895825
Pseudoboa nigra	AF544775	GQ457764	JQ598948	-	AF544729
Pseudoeryx plicatilis	GQ457826	GQ457765	GQ895885	-	GQ895826
Pseudoleptodeira latifasciata	EU728579	EU728579	EU728579	EU728579	-
Pseudotomodon trigonatus	GQ457827	GQ457766	-	-	GQ457887
Psomophis genimaculatus	GQ457828	GQ457767	-	-	GQ457888
Psomophis joberti	GQ457829	GQ457768	GQ895887	-	GQ895828
Psomophis obtusus	JQ598836	JQ598896	-	-	-
Ptychophis flavovirgatus	GQ457830	GQ457769	-	-	GQ457890
Rhachidelus brazili	JQ598837	JQ598897	JQ598952	-	-
Rhadinaea flavilata	-	-	AF471078	-	AF471152
Rhadinaea fulvivittis	-	-	EF078539	EF078587	-
Rodriguesophis iglesiasi	JQ598831	JQ598891	GQ895881	-	GQ895823
Sibon nebulatus	EU728583	EU728583	EU728583	EU728583	AF544736
Sibon noalamina	-	KP209376	-	-	-
Sibynomorphus mikanii	GQ457832	JQ627297	JQ598954	-	GQ457892
Sibynomorphus neuwiedi	JQ598838	JQ598898	-	-	-
Sibynomorphus turgidus	JQ598839	JQ598899	-	-	-
Sibynomorphus ventrimaculatus	JQ598840	JQ598900	-	-	JQ598997
Siphlophis cervinus	JQ598841	JQ598901	GQ895888	-	JQ598998
Siphlophis compressus	GQ457833	GQ457772	-	-	GQ457893
Siphlophis longicaudatus	JQ598842	JQ598902	-	-	JQ598999
Siphlophis pulcher	GQ457834	GQ457773	JQ598955	-	GQ457894
Sordellina punctata	JQ598843	JQ598903	JQ598956	-	JQ599000
Stichophanes ningshaanensis	KJ719252	KJ719252	KJ719252	KJ719252	KJ638718
Synophis bicolor MZUTI4180	-	KT944048	-	KT944065	KT944069
Synophis bicolor MHUA14577	KR814751	KR814758	KR814773	-	KR814769
Synophis bicolor MZUTI3529	-	KR814759	KR814771	KR814780	KR814762
Synophis bicolor MZUTI4175	-	KT944046	-	KT944063	KT944067
Synophis bicolor UTA R-55956	-	-	JX398697	JX398557	-
Synophis calamitus KU197107	KR814622	KR814640	KR814697	KR814711	KR814663
Synophis calamitus MZUTI3694	-	KR814755	KR814772	KR814774	KR814765
Synophis lasallei MZUTI4181	-	KT944047	-	KT944064	KT944068
Synophis zaheri MZUTI3353	-	KR814756	-	KR814776	KR814761
Synophis zaheri MZUTI3355	-	KR814757	-	KR814781	KR814763
Tachymenis peruviana	GQ457835	GQ457774	-	-	GQ457895
Taeniophallus affinis	JQ598844	JQ598905	JQ598957	-	GQ457853
Taeniophallus brevirostris	GQ457793	GQ457734	JQ598958	-	GQ457854

Species	**12S**	**16S**	**CYTB**	**ND4**	**CMOS**
Taeniophallus nicagus	JQ598845	JQ598906	-	-	JQ599001
Tantalophis discolor	-	-	EF078541	EF078589	-
Thalesius viridis	AF158468	AF158538	-	-	-
Thamnodynastes hypoconia	JQ598846	-	-	-	-
Thamnodynastes lanei	GQ457836	GQ457775	-	-	-
Thamnodynastes pallidus	GU018155	GU018166	-	-	-
Thamnodynastes rutilus	GQ457837	GQ457776	-	-	GQ457896
Thamnodynastes strigatus	JQ598847	JQ598907	JQ598959	-	-
Thermophis baileyi	-	-	EU864148	KF595097	EU496922
Thermophis zhaoermii	GQ166168	GQ166168	GQ166168	GQ166168	KF514882
Tomodon dorsatum	GQ457838	GQ457777	GQ895892	-	GQ895833
Tretanorhinus nigroluteus	-	-	GQ895893	-	GQ895834
Trimetopon gracile	GU018160	GU018178	-	-	-
Tropidodipsas sartorii	-	-	EF078540	EF078588	-
Tropidodryas serra	JQ598848	JQ598908	JQ598961	-	-
Tropidodryas striaticeps	GQ457839	GQ457778	AF236811	-	-
Uromacer catesbyi	AF158454	AF158523	FJ416714	FJ416788	-
Uromacer frenatus	AF158444	AF158513	FJ416715	FJ416789	-
Uromacer oxyrhynchus	FJ416701	FJ416712	FJ416716	FJ416790	-
Xenodon dorbignyi	GQ457812	GQ457752	-	-	GQ457872
Xenodon guentheri	JQ598849	JQ598909	-	-	-
Xenodon histricus	GQ457813	GQ457753	JQ598962	-	GQ457873
Xenodon matogrossensis	JQ598850	JQ598910	-	-	-
Xenodon merremi	GQ457840	JQ598911	JQ598963	-	GQ457898
Xenodon nattereri	JQ598851	JQ598912	-	-	-
Xenodon neuwiedii	GQ457841	GQ457779	AF236814	-	-
Xenodon pulcher	JQ598852	JQ598913	-	-	-
Xenodon semicinctus	GU018156	GU018173	GQ895877	-	-
Xenodon severus	JQ598853	Z46474	JQ598964	-	-
Xenopholis scalaris GFM825	-	JQ598915	-	-	-
Xenopholis scalaris JPV	GU018145	GU018164	-	-	-
Xenopholis scalaris KU222204	-	-	GQ895897	-	GQ895837
Xenopholis scalaris WED57797	JQ598854	-	-	-	JQ599002
Xenopholis undulatus R6955	JQ598855	JQ598916	-	-	JQ599003