

A remarkable record of the genus *Pseudolucia* from Bolivia (Lepidoptera: Lycaenidae)

J. F. GUERRA SERRUDO¹, G. SIEBEL², R. VILA³, D. BENYAMINI⁴ & ZS. BÁLINT^{5*}

¹Juan Fernando Guerra Serrudo, Investigador Asociado, Instituto de Ecología C.P. 10077 La Paz. Obrajes Calle 4 no' 320 Avenida H. Ormachea, La Paz, Bolivia. Email: ferguerrafideo@yahoo.com

²Gottfried Siebel, 6 de Agosto, 2636, 25/8 La Paz. Email: siebelg@yahoo.de

³Roger Vila, Institut de Biologia Evolutiva (CSIC-Universitat Pompeu Fabra), Passeig Marítim de la Barceloneta, 37, 08003, Barcelona, Spain. Email: roger.vila@csic.es

⁴Dubi Benyamini, 4D MicroRobotics, 91 Levona str. Bet Arye, Israel 7194700. Email: dubi_ben@netvision.net.il

⁵Zsolt Bálint, Department of Zoology, Hungarian Natural History Museum, Budapest VIII, Baross utca 13, H-1088, Hungary. Email: balint.zsolt@nhmus.hu, *corresponding author.

Abstract. The occurrence of a taxon morphologically close to *Pseudolucia jujuyensis* Bálint, Eisele & Johnson, 2000 is recorded in dry habitats of Torotoro Dinosaurs National Park, Potosí, Bolivia. This record remarkably extends the range of *Pseudolucia* by almost 800 km northwards in austral South America. Five specimens were available for examinations, hence wing-pattern, genitalia and mitochondrial DNA were analysed. However, the taxonomy of the specimens could not be satisfactorily resolved in relation to *P. jujuyensis*, for which only the holotype exists. The females use *Cuscuta* for ovipositing, what is supposedly the larval host – a remarkable character of the *chilensis* species group of *Pseudolucia*, which includes *P. jujuyensis*. On the basis of molecular markers it was revealed that the Torotoro population is the sister to the rest of the *chilensis* species group, which together are the clade sister to the rest of the genus.

Keywords. Andes, Argentina, Bolivia, butterfly, distribution, phylogeny, prepuna biome, *Pseudolucia*, systematics.

INTRODUCTION

The genus *Pseudolucia* represents the main South American endemic radiation of the lycaenid tribe Polyommatainae. When the genus was established by Vladimir Nabokov on the basis of two species, its distribution was believed to be restricted to a limited area in central Chile (Nabokov 1945). Since then, mainly based on the efforts of one of us (Benyamini), who led numerous expeditions to the austral South America, representatives of the genus have been recorded from the department Jujuy in the north of Argentina to Santa Cruz in the south, and in Chile from the Antofagasta (North of Atacama) region to the Magallanes (adjacent Tierra Del Fuego) region (Benyamini 2013, Bálint & Benyamini 2014).

After processing the material collected by these expeditions, the species in the genus have been raised to 55, more than one order of magnitude (Benyamini & Bálint 2015). Many formerly or newly described species have been sampled several times, but the species *Pseudolucia jujuyensis* Bálint, Eisele & Johnson, 2000, the most northerly member of the genus, remains an enigma. It was described on the basis of a single male specimen collected in 1977 in Coraya, Humahuaca, department of Jujuy, Argentina, but efforts aiming at its rediscovery turned to be unsuccessful (Benyamini & Bálint 2015). It is suspected that the singleton holotype was blown up or was a specimen performing hill-topping because there is no potential larval host plant in the area (tens of kilometres) around the biotope.

A recent expedition led by the senior author in Central Bolivia in order to search *Strymon heodes* (see Bálint & Benyamini 2017), resulted in the discovery of a *Pseudolucia* species in the region. This record is remarkable as it extends the range of the genus by almost 800 km northwards in austral South America. This is the single *Pseudolucia* species known to occur in Bolivia.

The aim of the present paper is to report and to document the discovery, and to discuss the identity of the specimens using morphological and molecular traits. We also annotate the biology of the closely related *Pseudolucia* species and stress the importance of the new record from a zoogeographic point of view.

MATERIALS AND METHODS

Four males and one female, all from Bolivia, Potosí, Torotoro Dinosaurs National Park, 2700–2850 m have been examined. Two males collected 30.III.2016 by G. Siebel (male: Dubi Benyamini's collection number 0300, RVcoll16M146; another male: deposited in the Hungarian Natural History Museum, RVcoll16M147); two males and one female collected 13.XII.2016 by J. F. G. Serrudo (all in Dubi Benyamini's collection, male numbers 0302-0303, RVcoll16M148-16M149, female: 0301, RVcoll16M150) (Table 1).

Because of the uncertainty of the relation of the discovered population to the holotype of *Pseudolucia jujuyensis*, we apply the informal name “torotorensis” for the Bolivian population. In this way, we want to stress the uniqueness of the population discovered, but it cannot be considered as a nomenclatorial or a taxonomic action. Therefore the name “torotorensis” is not available for the zoological nomenclature.

Adult behaviour and habitat were recorded in situ using digital cameras. Samples of adult butterflies, nectar-sources and supposed larval hosts were hand-collected by local scientists and desiccated. Subsequently they were transferred to Benyamini's laboratory and were databased there. Conservation, curation, dissection and setting of

the samples were done by traditional methods (Winter 2000). Adult wing margins were measured from digital images for comparing congeners following the protocol of Bálint *et al.* (2000). The measurements are given in Table 2. One male and one female *Pseudolucia* specimen have been dissected in the Hungarian Natural History Museum (Bálint genitalia preparation number 1618 for male DBC-302 and 1619 for female DBC-301), digitized and compared with congeners. Samples were also secured for molecular studies.

Molecular analyses have been carried out in the laboratory lead by Roger Vila (specimens examined are documented as RVcoll16M####; see above). Legs were taken from all individuals available of “torotorensis” and the mitochondrial marker *cytochrome c oxidase subunit I (COI)* was sequenced. The method used is described in detail by Talavera *et al.* (2013) and by Vodá *et al.* (2015). Also, a number of outgroup taxa within *Pseudolucia* were sequenced using the same protocol, as well as sequences available in GenBank for the 2172 bp fragment spanning markers *COI + leu-tRNA + COII* (Table 1). PCR products were purified and sequenced by Macrogen Inc. Sequences were edited and aligned using GENEIOUS PRO 6.0.5 created by Biomatters (<http://www.geneious.com/>). All new sequences have been deposited in GenBank (for accession numbers see Table 1). A Neighbour-Joining phylogenetic tree was obtained using a HKY distance model in GENEIOUS PRO 6.0.5, with 100 bootstrap pseudo-replicates to assess the robustness of the tree clades.

RESULTS AND DISCUSSION

Identification

(Figures 1–11)

The species collected in Bolivia belongs to the *chilensis* species group of *Pseudolucia* Nabokov, 1945 (type species: *Lycaena collina* Philippi, 1859) because the dorsal wing surfaces of both sexes have no structural colouration, the ventral hindwing pattern has no conspicuous median pat-

Table 1. Samples used in this study with the specimen codes, original localities and GenBank accession numbers.

Code	Species	Date	Locality	Country	Altitude (m.a.s.l.)	Collector	GenBank Acc. Num.
BD02B788	<i>Pseudolucia barrigai</i>	2001-12-25	Valle de las Leñas, Mendoza	Argentina	2310	D. Benyamini	GQ128995
BD02B792	<i>Pseudolucia shapiro</i>	2001-12-26	Valle de las Leñas, Mendoza	Argentina	2068	D. Benyamini	GQ129005
BD02B796	<i>Pseudolucia collina</i>	2001-12-27	Lago Alumine, Neuquén	Argentina	1233	D. Benyamini	GQ129000
BD02B797	<i>Pseudolucia grata</i>	2001-12-27	Lago Alumine, Neuquén	Argentina	1233	D. Benyamini	GQ129001
BD02B801	<i>Pseudolucia tamara</i>	2001-12-28	Río Trafal, 1 km NW Confluencia, Neuquén	Argentina	861	D. Benyamini	GQ129007
BD02B807	<i>Pseudolucia patago</i>	2001-12-30	Chile Chico, Aisén	Chile	240	D. Benyamini	GQ129004
BD02B812	<i>Pseudolucia vera</i>	2002-01-04	Volcán Villarica, Temuco, Araucanía	Chile	1432	D. Benyamini	GQ129008
BD02B813	<i>Pseudolucia charlotte</i>	2002-01-04	Temuco, Araucanía	Chile		D. Benyamini	GQ128998
MFB00N227	<i>Pseudolucia chilensis</i>	2000-12-01	Farellones, Santiago Metropolitan	Chile	1850	M.F. Braby	GQ128999
OM05G417	<i>Pseudolucia parana</i>	2004-03-02	Vila Velha, Parana	Brazil		O. Mielke	GQ129003
RV03V020	<i>Pseudolucia asafi</i>	2003-01-21	Céspedes, Illapel, Coquimbo	Chile	2650	R. Vila	GQ128997
RV03V073	<i>Pseudolucia henyah</i>	2003-01-26	Crtr.5 Km338, Fray Jorge, Coquimbo	Chile		R. Vila	GQ129002
RV03V101	<i>Pseudolucia annamaria</i>	2003-01-28	Alcohuás, Coquimbo	Chile	2000	R. Vila	GQ128996
RV03V112	<i>Pseudolucia sibylla</i>	2003-01-29	Río La Laguna, Paso del Agua Negra, Coquimbo	Chile	3700	R. Vila	GQ129006
RVcoll11J799	<i>Pseudolucia oligocyanea</i>	2011-10-20	22 km South Socaire, Antofagasta, Atacama	Chile	3650	D. Benyamini	MG783988
RVcoll12R451	<i>Pseudolucia balinti</i>	2011-07-09	Sierra del Tontal, Calingasta, San Juan	Argentina	3238	D. Benyamini	MG783986
RVcoll12R545	<i>Pseudolucia aureliana</i>	2012-12-09	ca. 10 km S. Inca de Oro, Copiapó, Atacama	Chile	2000	D. Benyamini	MG783985
RVcoll12R547	<i>Pseudolucia patago</i>	2012-12-13	Río Jeinimeni, Chile Chico, Aisén	Chile	240	D. Benyamini	MG783989
RVcoll12R549	<i>Pseudolucia maricunga</i>	2012-12-11	Cuesta Codoceo, Copiacó, Atacama	Chile	3933	D. Benyamini	MG783987
RVcoll16M146	<i>Pseudolucia "torotorensis"</i>	2016-03-30	Torotoro National park, Potosí	Bolivia	2700-2850	G. Siebel	MG783990
RVcoll16M147	<i>Pseudolucia "torotorensis"</i>	2016-03-30	Torotoro National park, Potosí	Bolivia	2700-2850	G. Siebel	MG783991
RVcoll16M148	<i>Pseudolucia "torotorensis"</i>	2016-12-13	Torotoro National park, Potosí	Bolivia	2700-2850	J.F.G Serrudo	MG783992
RVcoll16M149	<i>Pseudolucia "torotorensis"</i>	2016-12-13	Torotoro National park, Potosí	Bolivia	2700-2850	J.F.G Serrudo	MG783993
RVcoll16M150	<i>Pseudolucia "torotorensis"</i>	2016-12-13	Torotoro National park, Potosí	Bolivia	2700-2850	J.F.G Serrudo	MG783994



Figures 1-3. Genitalia of the Bolivian *Pseudolucia* specimens “torotorensis”. 1 = male, the whole organ in lateral view; 2 = male genitalia valva, in larger magnification; 3 = female genitalia ductus with sclerotized henia in dorsal view (scale bars = 0,8 mm) (photos: Hungarian Natural History Museum).

pattern (Figs. 1–8), male genitalia tegumen has a dorso-lateral projection, uncus lobe shape is securiform, aedeagus suprazonal portion is extremely short and pointed, the apex is pointed and the female genitalia ductus is heavily pleated (Figs. 1–3).

The following characters examined in the male and female “torotorensis” adults differ from *P. chilensis* and match well with the only known holotype specimen of *Pseudolucia jujuyensis*: (1) wing surfaces without orange scaling (*P. chilensis* with orange scaling), (2) hindwing ventral wing surface maculation without black scaling (*P. chilensis* with black scaling), and (3) male genitalia valva with angulated costa (*P. chilensis* costa non-angulated). These three observations suggest that the Bolivian “torotorensis” specimens are morphologically close to the holotype of *P. jujuyensis* (Figs. 4–11).

The traits of the “torotorensis” specimens that differ compared with *P. jujuyensis* holotype are the followings: (1) the ground colour and macu-

lation seem to be lighter and (2) male genitalia valva is slightly shorter. We do not have enough material for analysing the variability of these traits, but it is known that the first trait could be strongly influenced by temperature, as experiments carried on *Polyommatus icarus* (Rottemburg, 1775) have demonstrated (Kertész et al. 2016). The most striking character of the *P. jujuyensis* holotype in comparison with *P. chilensis* was the peculiar wing shape typified by the wing margin mean ratios 1.54/1.09 (see Bálint et al. 2000). Given the similarity to the ratios of the Bolivian specimens, 1.37/1.06, 1.53/1.07, 1.50/1.12 and 1.33/1.11 (cf. Table 2), this character seems not to support a species distinction at the moment, although we do not know the variability of the Jujuy population.

Summarizing all of these results, we can propose two alternative hypotheses: (1) the holotype of *P. jujuyensis* represents the same species observed on Torotoro, but it is an extreme individual collected at the very southern edge of the species’ range, or (2) the holotype of *P. jujuyensis*



Figures 4–7. Male *Pseudolucia* museum specimens documented under identical light conditions. 4–5: the holotype of *Pseudolucia jujuyensis*, 4 = in dorsal view, and 5 = in ventral view; 6–7: the HNHM specimen of “torotorensis”, 3 = in dorsal and 4 = in ventral view. (Scale bars 1mm) (photos: Katona Gergely).

Figures 8–11. Imagines of the Bolivian *Pseudolucia* specimens “torotorensis”, collected in Potosí, Torotoro National park, 2700–2850 m, 13.XII.2016 by J. F. G. Serrudo. 8 = male (DBC-0302) in dorsal view; 9 = ditto, in ventral view; 10 = female (DBC-0301) in dorsal view; 11 = ditto, in ventral view (forewing costa length 13 mm for Figs. 8–9 , and 12 mm for Figs. 10–11) (photos: Ofir Tomer).

Table 2. Forewing length measurements of *Pseudolucia* “torotorensis” individuals.

Catalog reference	Sex	Costal margin (A)	Outer margin (B)	Anal margin (C)
DBC-0300	M	11mm	8mm	8.5mm
DBC-0301	F	13mm	9.5mm	10mm
DBC-0302	M	12mm	8mm	9mm
DBC-0303	M	12mm	9mm	10mm
HNHM specimen	M	11mm	7.5mm	8mm

is a typical individual and the populations of Co-roya and Torotoro are specifically distinct. At this moment the material in our disposal is not enough to take a decision hence we provisionally regard the two populations as conspecific. For a final decision regarding their taxonomy the species *P. jujuyensis* has to be rediscovered and new samples analysed.

Molecular analysis

(Figure 12)

The molecular analysis of the genus using mitochondrial DNA shows that “torotorensis” belongs to the *chilensis*-group and forms a well-supported clade together with *P. chilensis* and *P.*

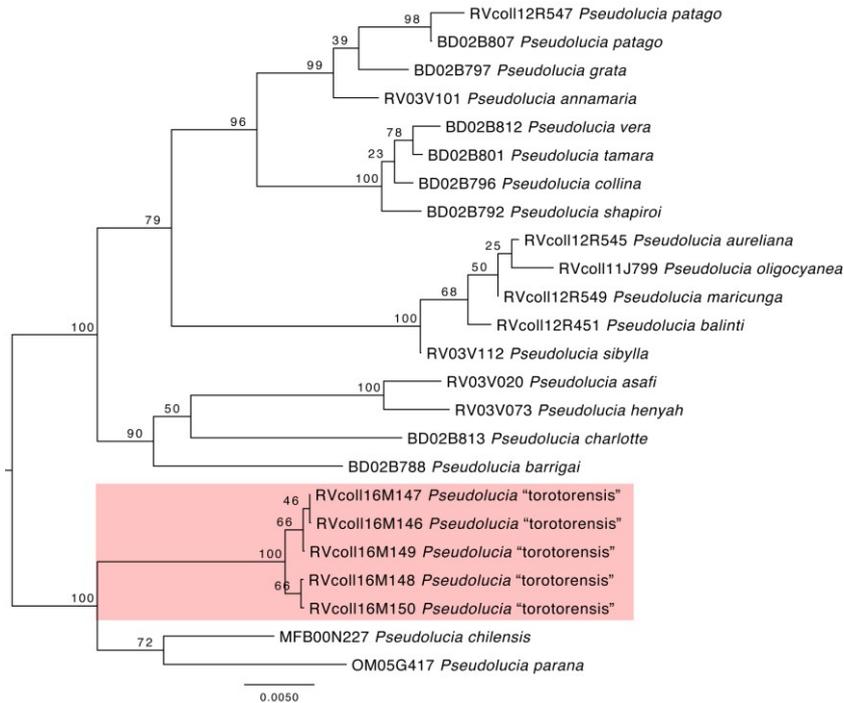


Figure 12. Neighbour-Joining tree for *Pseudolucia* based on mitochondrial sequences *COI* + *leu-tRNA* + *COII* with bootstrap values >50 indicated. Scale units are presented in substitutions per site. The *Pseudolucia* samples from Bolivia are highlighted.

parana. All five “torotorensis” specimens form a highly supported clade with little variability (a single substitution in *COI* shared by two specimens) that is sister to the clade including *P. chilensis* and *P. parana*. Specimens of “torotorensis” display uncorrected p-distances to the two sister species of between 2.1 and 3.2% for the *COI*, which translates to between 1 and 2 million years of isolation assuming a mitochondrial standard substitution rate ranging from 1.5% to 2.3% uncorrected pairwise distance per million years (cf. Brower 1994). Thus, “torotorensis” split before *P. parana* became isolated in the Atlantic region of Brazil, which happened approximately 1 million of years ago (divergences between *P. chilensis* and *P. parana* range between 1.7 and 2.0% for the *COI*).

We cannot know where *P. jujuyensis* and *P. sosneada* would fall in the phylogenetic tree, as the samples taken from the type material did not yield any results. But on the ground of morphology we suppose that *P. jujuyensis* is in sister relationship with “torotorensis”, as appears to be the same in regards to *P. chilensis* and *P. sosneada*.

Distribution and zoogeography

(Figures 13–14)

According to known distribution ranges of other *Pseudolucia* species an almost 800 km of latitudinal distance between the type locality of *P. jujuyensis* and the collecting site in Torotoro may indicate two distinct taxa. However, in 27th of December, 2016 the first author observed a *Pseudolucia* species in a locality 60 km north of the Argentine border which is about 400 km south of Torotoro (Fig. 13). This new location is in the vicinity of the Argentine town Tarija (approximate coordinates: 21° 28' 33" S 64° 48' 17" W) and is in halfway between Coraya (the type locality of *P. jujuyensis*) and Torotoro. Material or documentation of this putative population is still not available, but it was remarked that the observed specimen is similar to the species recorded in the vicinity of Torotoro.

However, knowing that *P. chilensis* has a similarly extended range along the Pacific coast of



Figure 13. Geographical locations of the two known occurrences of *Pseudolucia* in Bolivia (Torotoro, department Potosí and Tarija, department Tarija), and the most northern known occurrence of *Pseudolucia* in Argentina (Coraya, department of Jujuy, the type locality of *Ps. jujuyensis*).

Figure 14. The general distribution of the *chilensis* species group of *Pseudolucia* indicated by administrative regions of various countries. Light grey highlighted states in Brazil: *P. parana*; dark grey highlighted regions in Bolivia: “torotorensis” dark grey highlighted province in Argentina: *P. jujuyensis*; striped province in Argentina *P. sosneada*, and black highlighted regions in Chile: *P. chilensis*.

Chile, it cannot be excluded that *P. jujuyensis* possesses a similarly wide Eastern Andean distribution (cf. Bálint, Johnson & Eisele 2000) from the Torotoro region in Bolivia in the north to Jujuy province in Argentina in the south. The phenomenon that the ranges of hypothetical sister species inhabiting the Eastern and Western sides of the Andes are latitudinally shifted is well documented (see Shapiro 1991 and Benyamini 2013). Probably this phenomenon is observed here in the case of the *P. chilensis* and *P. jujuyensis* species pair (cf. Fig. 14).

Biology

(Figures 15–18)

All individuals were observed in the close vicinity of *Cuscuta globiflora* Engelmann, 1859, the presumed larval host plant. Indeed, all the members of the *chilensis*-group apparently specialize on *Cuscuta*.

The genus *Cuscuta* is parasitic on other plants, and it is widely distributed in the Potosí region causing considerable harms for Bolivian farmers (Figs. 15–16). Males are flying near the larval host plant waiting for females, and hilltop and display territorial behaviour along upper edges of slopes and ridges (Fig. 17). In the locality just 1 km out of the Torotoro village, where the species was recorded first, one male individual was fighting with *Strymon oribata* males patrolling the same ridge (Fig. 18).

The females fly around the presumed larval host plant and crawl deep possibly for laying eggs. The caterpillars supposedly feed on buds, flowers and fruits of *Cuscuta*, as do the closely related species in other regions. According to regional weather data, we believe that the species may have at least three annual generations and that the fully-grown larvae of the last brood diapause until the next spring (November–December).



Figure 15. The site where the first *Pseudolucia* individual has been recorded in Bolivia, 500 m south of Torotoro village (-18.141860 S, -65.760080 W); in front there is a shrub covered by *Cuscuta globiflora* (photo: D. Benyamini).

Figure 16. *Cuscuta globiflora* in the vicinity of Torotoro, Bolivia, developing buds and flowers, the diet of *Pseudolucia* caterpillars (photo: D. Benyamini).

Figure 17. The site where female and male *Pseudolucia* individuals occurred together, 1 km south of Torotoro village, ca. 2800 m; males were hilltopping and patrolling along the ridge edges with *Strymon oribata* males (photo: D. Benyamini).

Figure 18. Territorial male *Pseudolucia* “torotorensis” at the edge of a ridge, in the vicinity of Torotoro village, Bolivia (photo: D. Benyamini).

Closing remarks

The region of Torotoro is well known because of the finding of spectacular footprints of five different species of dinosaurs, but its Lepidoptera fauna is poorly explored. Nevertheless, the occurrence of *Pseudolucia* in Torotoro agrees with the existence of a peculiar biome in Bolivia, which also extends south to the northern provinces of Argentina, known as “prepuna” (Cabrera 2000; López 2000).

It seems that this biome, although poor in biodiversity compared to other Neotropical sites, has

a Lycaenidae fauna mainly composed by species endemic for the region such as *Madeleinea lea* Benyamini, Bálint & Johnson, 1995; *Rhamma lapazensis* (K. Johnson, 1992), *Strymon oribata* (Weymer, 1890) and *Thecloxurina cillutincare* (Draudt, 1919). Another example of lycaenid endemic to the prepuna ecoregion is an undescribed *Rhamma* (recorded as *Strymon heodes* by Serrudo 2013), which probably belongs to the *chilensis* mimicry ring (Benyamini 1995).

Further investigations are needed for mapping the boundaries and complexity of the butterfly fauna in this rarely explored part of the Neotropical region.

Acknowledgements – Genetic analyses were supported by projects CGL2016-76322-P (AEI/FEDER, UE) and 2014-SGR-1532 (Generalitat de Catalunya); Cecília Corbella helped in the laboratory. Professor Uzi Plitmann (The Hebrew University, Jerusalem), identified the *Cuscuta* species. Gergely Katona (Budapest, HHM) and Ofir Tomer (Bet-Arye, Israel) helped in the preparation of the figures. Zsolt Bálint was supported by the scientific OTKA programs K 111741 and K 115724.

REFERENCES

- BÁLINT, ZS. & BENYAMINI, D. (2013): *Pseudolucia maricunga* sp. n., a new high Andean butterfly from northern Chile (Lepidoptera, Lycaenidae, Polyommatainae). *Folia entomologica hungarica*, 74: 175–183.
- BÁLINT, ZS. & BENYAMINI, D. (2017): Corrected synonymies: the identities of *Strymon bicolor* (Philippi, 1859) and *Strymon heodes* (Drucem, 1919). *Opuscula Zoologica Budapest*, 48: 61–69. doi: [10.18348/opzool.2017.1.61](https://doi.org/10.18348/opzool.2017.1.61)
- BÁLINT, ZS., JOHNSON, K. & EISELE, R. (2000): Description of the sister species of *Pseudolucia chilensis* (Blanchard, 1852) (Lepidoptera: Lycaenidae). *Folia entomologica hungarica*, 61: 169–179.
- BENYAMINI, D. (1995): Synopsis of biological studies of the Chilean Polyommataini (Lepidoptera: Lycaenidae). *Reports of the Museum of Natural History, University of Wisconsin (Stevens Point)*, 52: 1–51.
- BENYAMINI, D. (2013): *Pseudolucia balinti* sp. n. of the *plumbea-sibylla* species group in Central-West Argentina (Lepidoptera: Lycaenidae: Polyommatainae). *Folia entomologica hungarica*, 74: 157–174.
- BENYAMINI, D. & BÁLINT, ZS. (2015): Descriptions of eight new *Pseudolucia* species from Argentina with an updated list of species distributed in the austral regions of South America (Lepidoptera, Lycaenidae: Polyommatainae). *Folia entomologica hungarica*, 76: 173–216.
- BROWER, A.V.Z. (1994): Rapid morphological radiation and convergence among races of the butterfly *Heliconius erato* inferred from patterns of mitochondrial-DNA evolution. *Proceedings of the National Academy of Sciences USA*, 91: 6491–6495. doi: [10.1073/pnas.91.14.6491](https://doi.org/10.1073/pnas.91.14.6491)
- CABRERA, A.L. (1976): *Regiones fitogeográficas argentinas*. Enciclopedia Argentina de Agricultura y Jardinería, Tomo II Fs. 1. Ed. ACME. Bs. As. Argentina, 85 pp.
- KERTÉSZ, K., PISZTER, G., HORVÁTH, ZS. E., BÁLINT, ZS. & BIRÓ, L.P. (2017): Changes in structural and pigmentary colours in response to cold stress in *Polyommatus icarus* butterflies. *Scientific Reports*, 17(7): 1118. doi: [10.1038/s41598-017-01273-7](https://doi.org/10.1038/s41598-017-01273-7)
- LÓPEZ, R.P. (2000): La prepuna boliviana. *Ecología en Bolivia*, 34: 45–70.
- NABOKOV, V. (1945): Notes on Neotropical Plebejinae. *Psyche*, 52: 1–61.
- SHAPIRO, A. (1991): The zoogeography and systematics of the Argentina Andean and Patagonian pierid fauna. *Journal of Research on the Lepidoptera*, 28(3): 137–238, 4 pls, 24 figs, 4 tabs.
- TALAVERA, G., LUKHTANOV, V.A., PIERCE, N.E. & VILA, R. (2013): Establishing criteria for higher-level classification using molecular data: the systematics of *Polyommatus* blue butterflies (Lepidoptera, Lycaenidae). *Cladistics*, 29: 166–192. doi: [10.1111/j.1096-0031.2012.00421.x](https://doi.org/10.1111/j.1096-0031.2012.00421.x)
- VODĀ, R., DAPPORTO, L., DINCĂ, V. & VILA, R. (2015): Why Do Cryptic Species Tend Not to Co-Occur? A case study on two cryptic pairs of butterflies. *PLoS One*, 10(2): e0117802. doi: [10.1371/journal.pone.0117802](https://doi.org/10.1371/journal.pone.0117802)
- WINTER, W.D. Jr. (2000): *Basic techniques for observing and studying butterflies & moths*. The Lepidopterists' Society Memoir Number 5. Lepidopterists' Society, Los Angeles, xviii + 444 pp.