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ECOSYSTEMS

Erotylina Curran (Coleoptera, Erotylidae, Erotylini): redescription of type species, potential species groups and diversity of color patterns

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Abstract: The colorful genus *Erotylina* Curran was proposed to include a group of species originally described in *Erotylus* Fabricius but differing by the lack of three longitudinal carinae on the tibiae. The taxonomy of *Erotylina* is mostly based on coloration while information on mouthparts, thorax, male and female abdominal terminalia remain unknown. In addition, little is known about the factors underlying coloration in *Erotylina* and Erotylidae in general. Here we redescribe the type species of *Erotylina*, *Erotylus leopardus* Lacordaire providing the first descriptions of several morphological structures, and new data on its geographical distribution. *Erotylus nicaraguae* Crotch is proposed as new junior synonymy of *E. leoparda*. Lectotypes are designated for the following species: *Erotylus leopardus* Lacordaire, *Erotylus nicaraguae* Crotch and *Erotylus confluens* Crotch. Based on the geographical records, specimen labels, literature and online environmental databases, we show that *E. leoparda* includes two discrete morphs distributed across a latitudinal gradient, with intermediate and continuous variations distributed across altitudinal and temperature gradients. The present study sheds light on the taxonomy of *Erotylina* and provides the first clearest evidence of a relation between coloration, latitude, altitude, temperature variations and the distributional patterns of a taxon in Erotylidae.

Key words: Coloration, Cucujoidea, Erotylinae, neotropical region, pleasing fungus beetles, systematics.

INTRODUCTION

Erotylinae (Coleoptera: Erotylidae) are the largest subfamily of Erotylidae consisting of five tribes and 2563 species (Leschen et al. 2010), a number underestimated based on recent discovery of new taxa (Skelley & Gasca-Álvarez 2020, examples in Pecci-Maddalena & Lopes-Andrade 2018a, 2020). Erotylini, mostly restricted to the Neotropical region, is the second most speciose tribe of Erotylinae with more than 700 species (see Alvarenga 1994), surpassed by Tritomini with more than 1000 species (Leschen et al. 2010). Although the monophyly of Erotylini is well supported by phylogenetic studies at the higher levels of classification (Węgrzynowicz 2002, Leschen 2003, Robertson et al. 2004), phylogenetic studies at the genus level are absent and revisionary studies are lacking for most taxa.

The genus *Erotylina* Curran, 1944 (Erotylini) includes 30 species (Alvarenga 1994). Curran (1944) proposed the genus for a group of species, originally described in *Erotylus* Fabricius, 1775, that differ by their smooth tibiae, lacking three longitudinal carinae. Curran included 20 species

in *Erotylina* (five new species described by him and 15 formerly placed in *Erotylus*). Subsequently, based only on Curran's tibial character, without additional comments, Alvarenga (1977) transferred 11 species from *Erotylus* to *Erotylina*. One of these, *Erotylus variegatus* Fabricius, 1781, was later returned to *Erotylus* by Alvarenga (1994). The only morphological information on species of *Erotylina* is in Curran (1944) and the short descriptions by 19th century taxonomists (e.g. Duponchel 1825, Guérin-Méneville 1841, Lacordaire 1842). These old descriptions are mostly based in coloration, with few comments on their morphology. Information on their mouthparts, thorax, male and female abdominal terminalia, and other structures, remain unknown.

The type species of *Erotylina*, *Erotylus leopardus* Lacordaire, 1842, from Mexico, resembles *Erotylina nicaraguae* (Crotch, 1873) from Nicaragua, in morphology and black pronotum. However, they differ in the elytral color pattern. According to Gorham (1888), *Erotylina nicaraguae* "seems probable that this is only a local variety of *Erotylus leopardus* in which the black markings are divided into spots by the geminate striae, so that the interstices between the second and third, and between the fourth and fifth are free from black marks, and the spots are thus clathrate. I see no other difference, as the bright orange color is repeated in a specimen from Chontales which is certainly *Erotylus leopardus*".

Later, Curran (1944) pointed out: "This species [*E. nicaraguae*] is similar to the variety *confluens* but is yellowish with the lateral margins of the elytra mostly reddish. I have not seen anything agreeing with the description but believe that it is merely a color variation of *leopardus*." Despite their suggestion, none of these authors proposed *E. nicaraguae* to be a synonym of *E. leoparda*, possibly because the typical *E. nicaraguae* and *E. leoparda* color patterns are discernible and are from different geographical localities. Also, specimens expressing intermediate states between these patterns were not properly examined by those authors.

Historically, use of coloration as a diagnostic trait has contributed to the taxonomic disarray in Erotylidae as there appears to be much plasticity in color patterns in some lineages (Robertson et al. 2004; examples in Skelley 1998a and Pecci-Maddalena & Lopes-Andrade 2018b). It is worth noting that genetics and environmental effects on coloration in insects were unknown at the time of Gorham, Curran and other earlier taxonomists. Recent work identified eight genes that play a crucial role in insect cuticular pigmentation and sclerotization process (Sugumaran & Barek 2016). Color variations may also be a consequence of a temperature-dependent polyphenism, as is the occurrence of conspecific butterflies with two seasonal phenotypes (Gilbert 2001). Another interesting process is the clinal melanization within and among populations or closely related species across altitudinal or latitudinal gradients (Trullas et al. 2007, De Souza et al. 2017, Pecci-Maddalena & Lopes-Andrade 2017). In these cases, individuals inhabiting cold climates (usually higher altitudes and/or latitudes) are darker than populations distributed in lowlands, warmer climates or lower latitudes. Those geographical clines provide good evidences of the relationship between melanism and temperature, one of the key assumptions of a more complex phenomenon named "thermal melanism hypothesis" (Trullas et al. 2007).

Despite the theoretical and empirical evidence, studies attempting to explain the diversity of color patterns in Erotylidae need to be conducted. Although the occurrence of clinal variations have been reported for some species

(Boyle 1956, Skelley 1998a), as well the data on the "elevation" from some localities (Skelley & Cekalovic 2001, Skelley 2009), to our knowledge, there is no published work providing clear evidence of a relation between color patterns and different environmental factors (elevation, latitude and temperature) for any the taxa within this family.

The purposes of this work are twofold:

(1) To redescribe *Erotylina leoparda* (Lacordaire, 1842), providing the first description for mouthparts, thoracic structures, male and female abdominal terminalia, and new data on its geographical distribution. Based on comparisons of the male abdominal terminalia and other structures, *Erotylus nicaraguae* Crotch, 1873 is proposed as a new junior synonym of *Erotylina leoparda*. Lectotypes are designated for the following species: *Erotylus leopardus* Lacordaire, 1842, *Erotylus nicaraguae* Crotch, 1873 and *Erotylus confluens* Crotch, 1876.

(2) Based on the geographical distribution of *E. leoparda*, specimen labels, literature, and online environmental databases, we evaluate if different color patterns have distinct distributions and if the observed phenotypic variation may be distributed across a latitudinal, altitudinal and/or temperature gradients.

MATERIALS AND METHODS

Taxonomical and morphological studies

Materials reported in this work are deposited in the following collections (collection curators and assistants are in parentheses):

BMNH The Natural History Museum (London, United Kingdom; Maxwell Barclay)

CEMT Setor de Entomologia da Coleção Zoológica da Universidade Federal de Mato Grosso (Cuiabá, Mato Grosso, Brazil; Fernando Z. Vaz-De-Mello)

DZUP Coleção Entomológica Padre Jesus Santiago Moure, Universidade Federal do Paraná (Curitiba, Brazil; Lúcia Massutti de Almeida)

FSCA Florida State Collection of Arthropods (Gainesville, Florida, USA; Paul Skelley)

MNHN Muséum National d'Histoire Naturelle (Paris, France; Thierry Deuve)

MRSN Museo Regionale di Scienze Naturali (Torino, Italy; Fulvio Giachino)

UMZC University Museum of Zoology Cambridge (Camdridge, UK; Edgar Turner and Russell Stebbings)

In compliance with the Article 74 of the International Code of Zoological Nomenclature (ICZN 1999), a lectotype is designated for species names clearly based on syntypes, but also in the cases where the author did not state how many specimens were in the type series.

Dissection of specimens followed the methods provided by Pecci-Maddalena et al. (2019) and Skelley & Gasca-Álvarez 2020). Transcription of labels followed Pecci-Maddalena et al. (2019). Photographs courtesy of Jean-hervé Yvinec (Figure 1a–c) were taken with a Canon EOS 70D camera through a Canon MPE 65 lens. Photographs by PES were taken using a Syncroscopy Auto-Montage system with a JVC 3-CCD, KY-F75U digital camera through a Leica Z16 APO lens (Figures 2c–e; 4b'and 4g; 5a; 8a–e, 8h–l; 9a–f, h, j, o–p). The remaining photographs were taken by ISCPM with a Canon EOS 70D camera through a Tamron 90mm macro/Canon lens and Helicon Remote 3.9.11W software. Stacks of photographs were combined into one sharp image using Helicon Focus Pro 7.6.1 Pro (Helicon Soft Ltd, Kharkov, Ukraine) software. Terms for external morphology follow Lawrence et al. (2011) and McHugh et al. (1997). Descriptions of mouthparts and abdominal terminalia were based on Węgrzynowicz (2002),

Figure 1. Type material examined. a–b. Drawers from Oberthür collection (MNHN). c. Lectotype of *Erotylus leopardus* Lacordaire, 1842 (MNHN). d. Lectotype of *Erotylus confluens* Crotch, 1876 (UMZC). e–f. Lectotype of *Erotylus nicaraguae* Crotch, 1876 (UMZC). Scale bars: e = 1 mm.

Lawrence et al. (2011) and Pecci-Maddalena et al. (2019). The term "subgenal braces" proposed by Węgrzynowicz (2002), here refers to the ventral projections of the genae, more or less developed (most prominent in Encaustini). The term "postmandibular lobes" proposed by Boyle (1956), refer to a carinate lobe, more or less developed, projecting laterally from the subgenal brace forming one side of a groove in which the antennal base rests when retracted (most prominent in Tritomini). The following images do not include a scale bar: Figures 1c–d; 9a–f, 9j and 9o–p.

The following abbreviations are used herein: BW—width of the anterior edge of the scutellar shield; CL—length of the antennal club (measured from base of the eighth antennomere to apex of the eleventh antennomere); EL—elytral length (at midline, from anterior edge of scutellar shield to elytral apex); EW—greatest elytral width (across both elytra); GD—greatest depth of the body (from top of elytra to bottom of metaventrite); GW—greatest diameter of the eye (lateral view); PL—pronotal length along midline; PW—greatest pronotal width; TL—total length (= EL+PL; head not included). All measurements are given in millimeters. The ratio GD/EW was

Figure 2. Specimens of *Erotylina leoparda* (Lacordaire, 1842) from different localities. a–e. Dorsal view: A. Male from Jalapa (Mexico) (DZUP); b. Female from Cordoba (Mexico) (DZUP); c. Male from Ocotal Chico (Mexico) (FSCA); d. Male from Guanacaste (Costa Rica); e. Male from Braulio Carrillo National Park (Costa Rica) (FSCA). f. Lateral view of the specimen from Jalapa. g–h. Ventral views of the specimens from Jalapa and Cordoba, respectively. i. Pronotum and head of the specimen from Jalapa. Scale bars: a–i = 1 mm.

recorded as an indication of degree of convexity; TL/EW—indicates degree of body elongation. Measurements were taken from a female of *E. leoparda* from Xalapa, Mexico.

Geographical and climatic data

The distribution map was created using latitude and longitude coordinates estimated by tracking localities in the online database GeoNames (Wick 2012) and plotted on a map using the freeware QGIS 2.12.2. The geographical data presented here and those available in literature (Lacordaire 1842, Gorham 1888, Curran 1944, Delgado & Navarrete-Heredia 2011) were included on the map. Information on localities mentioned by Gorham (1888) was obtained from Selander & Vaurie (1962). When only the country, state or provinces were known, without more accurate location information, a question mark was included on the map. Localities in the maps were represented by an Arabic numeral using an image editing program.

The altitude map was created using digital elevation models (SRTM30 dataset. CGIAR-SRTM with 30 seconds resolution) and different shape files available at http://www.diva-gis.org/Data (Jarvis et al. 2008). The temperature map was created using WorldClim Bioclimatic variables at a spatial resolution of 2.5 arcmin for WorldClim version 2 (available at www.worldclim.org). The GeoTiff file corresponds to the annual mean temperature for the years 1970–2000. Accurate geographic records, including the exact sampling point or locality, were included in the Table I, together with altitudinal data obtained from the specimen's labels, scientific literature, or Google Earth website (available at https://earth.google.com/web/). Measurements in feet were transformed in meters. Information on average temperatures for each locality was obtained from the Climate-Data.org database (available in en.climate-data.org, weather data collected between 1982 and 2012) or in the scientific literature. Other specific information present in Table I were including in square brackets. Numbers in the legends of Figs. 8–9 correspond to the numbers presented in the Table I to readily associate specimen data (Table I) to its color pattern (Figs. 8–9).

The term "morph" and "variation" are used here following the scheme from Briolat et al. (2019, Fig. 2 from their study), i.e., "morph" refers to a phenotypically discrete population and "variations" refer to the differences between two morphs along an environmental gradient. For the proposal of the present study, the "*leoparda*" and "*nicaraguae*" morphs were defined based on the epipleuron coloration, as follows: yellow in the "*leoparda*" and orange in the "*nicaraguae*" populations. Following this definition, the specimens described by Gorham (1888, pg. 102) as "*Erotylus leopardus*" from Chontales and from "Cache" (Cachí, Costa Rica) "of a bright orange-yellow with rufous margins and epipleurae", here were considered "*nicaraguae*".

Other geographical records of *E. leoparda* and *E. nicaraguae*, including images, can be accessed on the website inaturalist.org (available at https://www.inaturalist.org/). These records were studied. Since we cannot confirm their accuracy, they are not included in the examined material. However, their geographical data and color patterns agree with the findings of the present study.

RESULTS

Erotylina leoparda (Lacordaire, 1842)

Erotylus leopardus Lacordaire 1842: 442 [description]. Crotch 1876: 531; Gemminger & Harold 1876: 3714; Gorham 1888: 102; Kuhnt 1908: 96, 1909: 37, 1911: 24; Deelder 1942: 65; Curran 1944: 6 [transfer to *Erotylina*; without adding the suffix "-a" to "*leopardus*" to make it feminine];

Table I. Elevation (m) and annual mean temperature (°C) from localities where the two morphs of *Erotylina leoparda* (Lacordaire, 1842) ("*leoparda*" and "*nicaraguae*") were collected. Specific information, sources, etc., are in square brackets. Data are organized by country and under a gradient of elevation.

Number on Figs. 6–9	Phenotype	Source	Country	Provenance	Elevation (m)	Temperature (°C)	Collect (label data)
1	*nicaraguae*	Material examined (present work)	Costa Rica	El Ceibo Station, Braulio Carrillo National Park (Heredia and San Jose, Costa Rica)	400-600 [label data]	20.6 and 20.9 [Data from Heredia and San Jose, respectively]	FEB-1990
2	*nicaraguae*	Gorham (1888)	Costa Rica	Cachí (Cartago, Costa Rica)	609 [Selander & Vaurie 1962]	21	NA [drawer level image, labels not examined]
3	*nicaraguae*	Material examined (present work)	Costa Rica	Estacion Biologica Pitilla (Guanacaste, Costa Rica)	700 [label data]	25.8 [Data from Liberia the nearest city in the same climatic region]	18-APR-1993-19-MAY-1993
4	*nicaraguae*	Material examined (present work)	Costa Rica	San Luis (Monteverde, Punta Arenas, Costa Rica)	1040 [label data]	18.8 [Data from Monteverde (Nadkarni & Wheelwright 2000)]	MAY-1993
5	*nicaraguae*	Material examined (present work)	Costa Rica	Ecolodge San Luis, University of Georgia's Costa Rica Campus (Monteverde, Punta Arenas, Costa Rica)	1000-1350 [label data]	18.8 [Data from Monteverde (Nadkarni & Wheelwright 2000)]	22-24-JUN-2003
6	*nicaraguae*	Material examined (present work)	Costa Rica	Santa Elena (Punta Arenas, Costa Rica)	1305 [label data]	19	9-12-JUN-1986
7	*nicaraguae*	Crotch (1873); Gorham (1888); Material examined (present work)	Nicaragua	Santo Domingo (Chontales, Nicaragua)	868 [Selander & Vaurie 1962]	23.3	NA
8	*nicaraguae*	Material examined (present work)	Nicaragua	Mombacho Volcano Natural Reserve (Granada, Nicaragua)	1150 [label data]	~17–21.2 at 1200m [Weaver & Santos 2002]	2-JUN-2002

Table I. Continuation

Number on Figs. 6–9	Phenotype	Source	Country	Provenance	Elevation (m)	Temperature (°C)	Collect (label data)
9	*nicaraguae*	Material examined (present work)	Nicaragua	Cerro Jesus (Nueva Segovia, Nicaragua)	1300 [label data]	19 [Veijalainen et al. 2014]	7-13-JUN-2015
10	*leoparda*	Material examined (present work)	Honduras	Zamorano Pan-American Agricultural School, EAP, San Antonio de Oriente, Francisco Morazán (Honduras)	807 [Google Earth]	20.1	9-JUN-1982
11	*leoparda*	Material examined (present work)	Honduras	Güinope (El Paraíso, Honduras)	1307 [Google Earth]	21.1 [Cornacchia et al.1998]	26-JUL-1988
12	*leoparda*	Material examined (present work)	Honduras	Ridge between La Montañita and C. Uyuca, about 5 km Southwest of Suyapa (Morazán, Honduras)	1584-1645 [label data]	?	5-AUG-1948
13	nicaraguae	Material examined (present work)	Honduras	Boquerón (Olancho, Honduras)	1157 ["Boquerón" Google Earth]	?	1-4-JUN-1995
14	*leoparda*	Gorham (1888)	Guatemala	Cubilguitz (Alta Verapaz, Guatemala)	320 [Selander & Vaurie 1962]	?	NA [drawer level image, labels not examined]
15	leoparda	Gorham (1888)	Guatemala	Sinanjá (Baja Verapaz, Guatemala)	432 [Google Earth]	?	NA [drawer level image, labels not examined]
16	*leoparda*	Gorham (1888)	Guatemala	Panimá (Baja Verapaz, Guatemala)	548 [Selander & Vaurie 1962]	?	NA [drawer level image, labels not examined]
17	leoparda	Gorham (1888)	Guatemala	El zapote (Escuintla, Guatemala)	609 [Selander & Vaurie 1962]	?	NA [drawer level image, labels not examined]

Table I. Continuation

Number on Figs. 6–9	Phenotype	Source	Country	Provenance	Elevation (m)	Temperature (°C)	Collect (label data)
18	*leoparda*	Gorham (1888)	Guatemala	Senahú (Alta Verapaz, Guatemala)	1173 [Selander & Vaurie 1962]	21.7	NA [drawer level image, labels not examined]
19	leoparda	Material examined (present work)	Guatemala	Purulhá (Baja Verapaz, Guatemala)	1563 [Google Earth]	16.9	21-NOV-2008
20	*leoparda*	Material examined (present work)	Mexico	Ocotal Chico (Soteapan, Veracruz, Mexico)	579 [label data]	23.3 [Data from Soteapan]	I-JUN-1965
21	*leoparda*	Material examined (present work)	Mexico	Cordoba (Veracruz, Mexico)	830 [Google Earth]	21.1	16-AUG-[YEAR?]
22	*leoparda*	Material examined (present work)	Mexico	Between Fortin de las Flores and Sumidero (Veracruz, Mexico)	762–914 [label data]	20.4 [Data from Fortin de las Flores]	14-JUL-1968
23	*leoparda*	Material examined (present work)	Mexico	Jalapa (Veracruz, Mexico)	1426 [Selander & Vaurie 1962]	18.2	NA
24	*leoparda*	Gorham (1888)	Mexico	Santa Catarina Juquila (Oaxaca, Mexico)	1493 [Selander & Vaurie 1962]	20.4	NA [drawer level image, labels not examined]
25	*leoparda*	Delgado & Navarrete-Heredia (2011)	Mexico	Banderilla (Veracruz, México)	1500 [Google Earth]	17.4	Image available in Delgado & Navarrete-Heredia 2011. [Color pattern = specimens from Jalapa]
26	*leoparda*	Material examined (present work)	Mexico	Lagunas de Montebello National Park (Chiapas, Mexico)	1524 [Coleman & Seybold 2011, same sample]	23.6 [average monthly temperature, CONANP 2007]	21-JUN-1990

Blackwelder 1945: 461 [checklist; did not include the name "*Erotylina*", species are listed under *Erotylus*]; Alvarenga 1994: 100 [catalogue]; Skelley 1998b: 31 [catalogue]; Delgado & Navarrete-Heredia 2011: 461 [*Erotylina leoparda*].

Erotylus confluens Crotch 1876: 531 [description]. Gemminger & Harold 1876: 3713; Gorham 1888: 102 [junior synonym]; Curran 1944: 9; Blackwelder 1945: 460; Alvarenga 1994: 100 [catalogue]; Skelley 1998b: 31 [catalogue].

Erotylus nicaraguae Crotch 1873: 148 [description]. Crotch 1876: 532; Gemminger & Harold 1876: 3714; Gorham 1888: 102; Kuhnt 1908: 96, 1909: 37, 1911: 24; Curran 1944: 9 [transfer to *Erotylina*]; Blackwelder 1945: 461 [listed under *Erotylus*]; Alvarenga 1994: 100 [catalogue]; Skelley 1998b: 31 [catalogue]. **New synonym.**

Type material examined. Lectotype of *Erotylus leopardus* Lacordaire, 1842, here designated (MNHN); Figure 1c**).** "Erotylus leopardus [?], Lac., Mexique, Type [handwritten] \ [other labels not examined]". **Lectotype of *Erotylus nicaraguae* Crotch, 1873, here designated (UMCZ);** Figure 1e–f**).** "TYPE [blue label, printed] \ TYPE. [printed], Nicaraguae, Chont. [handwritten]". **Lectotype of *Erotylus confluens* Crotch, 1876, here designated (UMCZ);** Figure 1d**).** "TYPE [blue label, printed] \ TYPE. [printed], Confluens, Mex. [handwritten]".

Other specimens examined. *Eroylina leoparda* (Lacordaire, 1842): 29 specimens, labels not examined, sex undetermined (BMNH, drawer level image); 4 specimens, labels not examined, sex undetermined (MNHN, drawer level image); 1 specimen, unlabeled, sex undetermined (MRSN, drawer level image); 1 specimen, sex undetermined (UMZC) "Mexico [red label, handwritten] \ TYPE. [crossed out, printed], leopardus [handwritten]"; 1 specimen, unlabeled, sex undetermined (UMZC); 2 specimens, labels not examined, sex undetermined (UMZC); 1 male (DZUP, dissected) "Jalapa, Mexico., Hoege. [printed; material from Biologia Centrali Americana, Gorham (1888)] \ Coleção M. Alvarenga [printed] \ DZUP 229525 [printed]"; 1 female (DZUP, dissected) "Coleção M. Alvarenga [printed] \ *Erotylina leopardus* (Lac. 1842) [handwritten], M. Alvarenga det. 1971 [printed] \ Cordoba VC [printed], 16.08 [?, handwritten], Mex [printed] \ FredkKnab Collector [printed] \ 926 [printed] \ DZUP 229523 [printed]"; 1 male (FSCA, dissected) "Ocota, Chico, 1900' [handwritten] \ MEXICO: Veracruz [printed], I June [handwritten], 1965, G.N. Ross # [printed] \ G.N. Ross colln., MGCL Accession, # 2006–20 [printed]"; 1 female and 1 male (FSCA) "MEXICO: Chiapas, Laguna Montebello, Parq. Nac., 21-VI-1990, coll. M. C. Thomas"; 1 female (FSCA) "MEXICO: State of, Veracruz, Fortin, de las Flores - , Sumidero \ Planta de la, Cerveceria, Ing., Daniel Rábago res., elev. 2500-3000' \ H. V. Weems, Jr., col. 14-VII-[19]68"; 1 male (FSCA) "10M: HONDURAS: Dept. MORAZÁN, Ridge betw. La Montañita, & C. Uyuca, 5±kmSW Suyapa, 5200-54400' Aug. 5, 1948, (pinabetál) Hubbel 195"; 1 male (FSCA) "11M: HONDURAS, Yoro, Abr 1982, E. Mendoza \ Fia. VII.93, No. 10"; 1 female (FSCA) "Reintsch, ex tomato / HONDURAS: EAP / 30km E. Tegucigalpa / 9-VI-1982 / Reintsch, ex tomato"; 1 male and 1 female (FSCA) "HONDURAS: El Paraiso, Guinope, 26 July 1988, J. Ordoñez colr"; 1 male (FSCA) "GUAT. BAJA VERAPAZ: / 8 km n. Purulha; beating: / oak forest; 21.ix.2008; / E. Fuller"; 1 female (CEMT) "MEX: VER, Xalapa – In Ecol, VI. 2004, VdM [handwritten]".

***Erotylina nicaraguae* (Crotch, 1876):** 1 paralectotype, sex undetermined, here designated (BMNH, drawer level image) "Type [disc-shaped label] \ [other labels not examined]"; 1 specimen, labels not examined, sex undetermined (BMNH, drawer level image); 1 male (FSCA, dissected) "Est. El Celbo, P.N. Braulio, Carrilo 400–600m, Prov. Here., COSTA RICA, C. Chaves, Feb 1990., L-N-256500, 527700 [printed]

\ COSTA RICA, INBIO, CRI000, 347275 [printed]"; "1 male (FSCA, dissected) "Est. Pitilla, 700 m, 9 km S Sta., Cecilia, P.N. Guanacaste, Prov. Guan., COSTA RICA. 18 abr a 19, may1993. P. Ríos., L–N–330200, 380200 [printed] \ COSTA RICA, INBIO, CRI001, 397152 [printed]"; 1 female (FSCA) "San Luis, 1040 m, R. G., Monteverde, Prov. Punt., COSTA, RICA. May 1993. Z. Fuentes., L-N-250850, 449250 \ [bar code label] COSTA RICA INBIO, CRI001, 371128"; 1 male (FSCA) "Buen Amigo, San Luis Monteverde, A. C., Arenal, Prov., Punta. COSTA RICA. 1000-, 1350m. May 1994, Z Fuentes, L N, 250850_449250 # 2926 \ [bar code label] COSTA RICA INBIO, CRI001, 894364"; 1 female (FSCA) "COSTA RICA, Puntarenas Province, San Luis, Ecolodge San Luis (UGA) \ (22-24)-VI-2003, N. H. Nazdrowicz, N10 16.93' W84 47.93"; 1 female (FSCA) "COSTA RICA: Puntarenas:, 6 km. S. E. Santa Elana, 9-12 JUN 1986, F. T. Hovore, P. H. Sullivan"; 1 female (FSCA) "NIC: Nueva Segovia, Cerro Jesus, 1300m, VI/7-13/2015, Morris & Wappes"; 1 female (FSCA) "HONDURAS Olancho, Boquerón, June 1-4, 1995, Wells-Bonta-Selby"; 1 female (FSCA) "#16F: NICARAGUA: Granada Dept., Res. Nat. Volcan Mombacho, 1150m 11°50.05'N 85°58.83'W, 2-VI-2002, R. Brooks, Z. Falin, S. Chatzimanolis ex pyrethrum, fogging fungusy logs NIC1BFC02 147 \ [bar code label] SMO531846, KUNHM-ENT"; 1 male (FSCA) "#17M: NICARAGUA: Granada Dept., Res. Nat. Volcan Mombacho, 1150m 11°50.05'N 85°58.83'W, 2-VI-2002, R. Brooks, Z. Falin, S. Chatzimanolis ex pyrethrum, fogging fungusy logs NIC1BFC02 147 \ [bar code label] SMO531855, KUNHM-ENT"; 1 male (FSCA) "NICARAGUA: Granada Dept., Res. Nat. Volcan Mombacho, 1150m 11°50.05'N 85°58.83'W, 4-VI-2002, R. Brooks, Z. Falin, S. Chatzimanolis ex pyrethrum, fogging fungusy logs NIC1BFC02 186 \ [bar code label] SMO557319, KUNHM-ENT"; 1 male (FSCA) "NICARAGUA: Granada Dept., Res. Nat. Volcan Mombacho, 1150m 11°50.05'N 85°58.83'W, 4-VI-2002, R. Brooks, Z. Falin, S. Chatzimanolis ex pyrethrum, fogging fungusy logs NIC1BFC02 186 \ [bar code label] SMO557317, KUNHM-ENT".

***Erotylus giganteus* (Linnaeus, 1758):** 1 specimen, sex undetermined (DZUP) "Coleção M. Alvarenga [printed] \ OBIDOS, Pará, BRASIL [printed], X. 1962, J. Brazilino [handwritten] \ giganteus L. [handwritten] \ 884 [printed] \ DZUP 229521 [printed]".

Diagnosis. *Erotylina leoparda* differs from the other congeneric species by the combination of the following characters: (i) "*leoparda*" morph (e.g. Figures 1a–c; 3a–b, color patterns diagram), elytral color pattern black with yellow elytral spots confluent but not completely fused; elytral epipleuron yellow. (ii) "*nicaraguae*" morph (e.g. Figures 1d–e; 3c, color diagram), elytral color pattern with circular yellow spots completely fused and transverse elytral black marks, arranged more or less symmetrically (e.g. Figure 1e) or, similar to "*leoparda*" members, with a black background and yellow elytral spots somewhat confluent, but not completely fused (e.g. Figure 8c–d); lateral edge of elytra and epipleuron orange (Figure 8). Additional characters: tibiae thin, smooth, lacking longitudinal carinae (Figure

Figure 3. Examples of color pattern variations in *Erotylina leoparda* (Lacordaire, 1842). a–b. "*leoparda*" variations. c. "*nicaraguae*" variation. Arrows indicate plasticity among patterns.

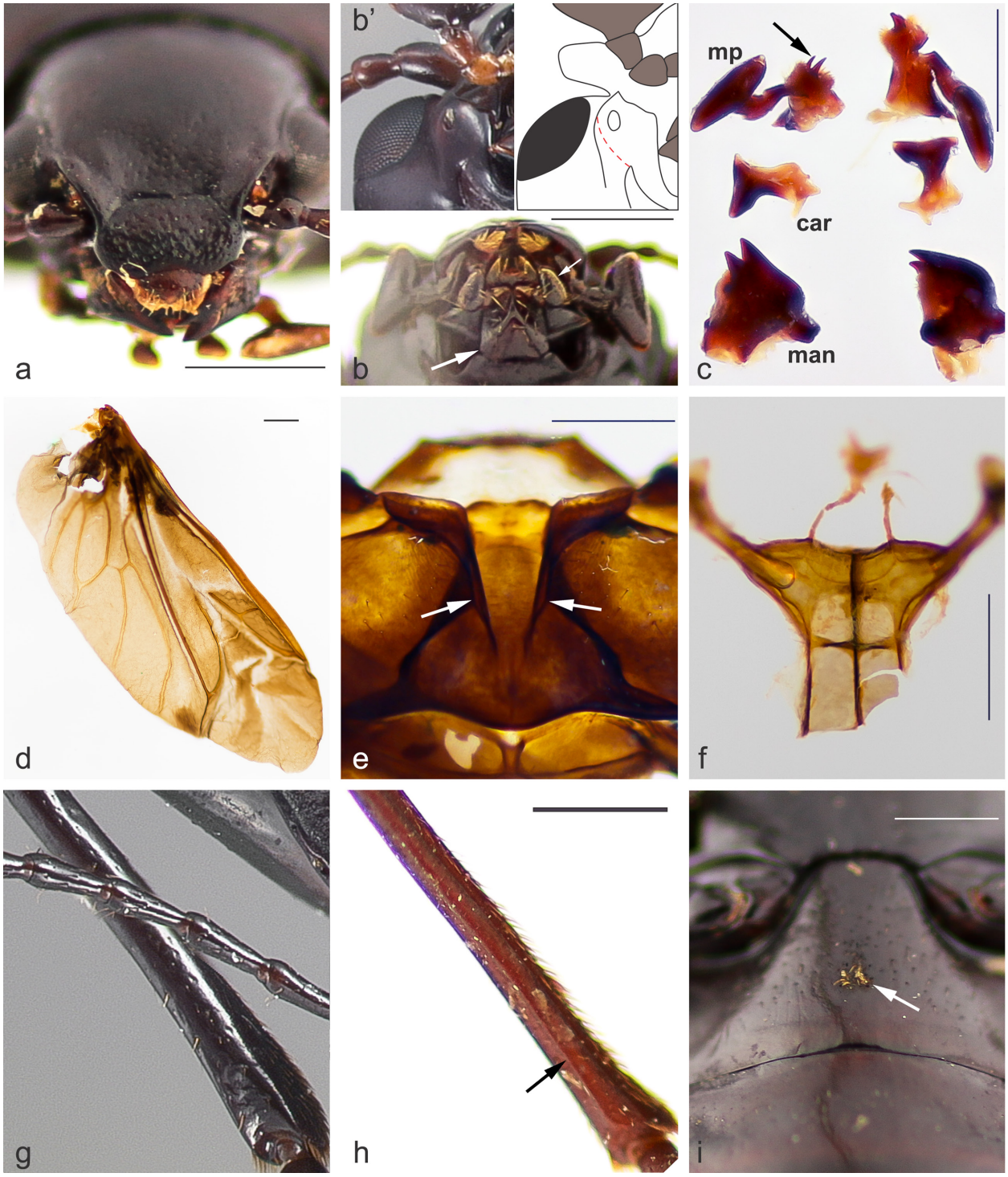

Figure 4. Adult morphology of *Erotylina leoparda* (Lacordaire, 1842). a. Epistome. b. Mouthparts, big arrow showing mentum plate, small arrow the labial palp. b'. Diagram showing subgenal braces, black outer contour "diverging" from red dashed line. c. Mandibles (man), cardo (car), apical maxillary palpomere (mp), arrow showing pair of hooks on lacinia. d. Metathoracic wings. e. Metanotum, arrows showing outer margin of metascutellum not touching posterior margin of metascutum. f. Metendosternite. g. Protibia lacking longitudinal carinae. h. Mesotibia of *Erotylus giganteus* (Linnaeus, 1758), arrow showing medial carina. i. Abdominal ventrite I of a male *E. leoparda* specimen, arrow showing a patch of setae. Scale bars: a–f, h–i = 1 mm.

4g). Penile flagellum (in male genitalia) with virga swollen close to flagellar head and thin medially and apically; flagellar head U-shaped or horseshoe-shaped (Figure 5b). Distribution: Mexico and Central America (Figures 6–7).

The "*leoparda*" morph is mostly distributed at high latitudes, across the Mexican transition zone (sensu Morrone 2014, see Discussion), in Mexico, Guatemala and part of Honduras (Figures 6–7). The "*nicaraguae*" morph occurs mostly in Costa Rica and Nicaragua, with a single record from Honduras (Figures 6–7). Under each of these discrete phenotypes, most specimens collected at higher elevations (and lower temperatures), have the yellow elytral spots more distinct and darker elytra (e.g. Figures 8c–e; 9j–n; Table I), compared to individuals collected at lower elevations (and warmer temperatures) with more fused elytral spots and yellow elytra (e.g. Figures 8a–b, f; 9a, h; Table I).

Description. TL = 13.19 mm. Body elongate, slightly oval, TL/EW = 1.21, GD/EW =0.57, glabrous, glossy dorsally, with few minute slender setae ventrally; dorsal and ventral coloration as in

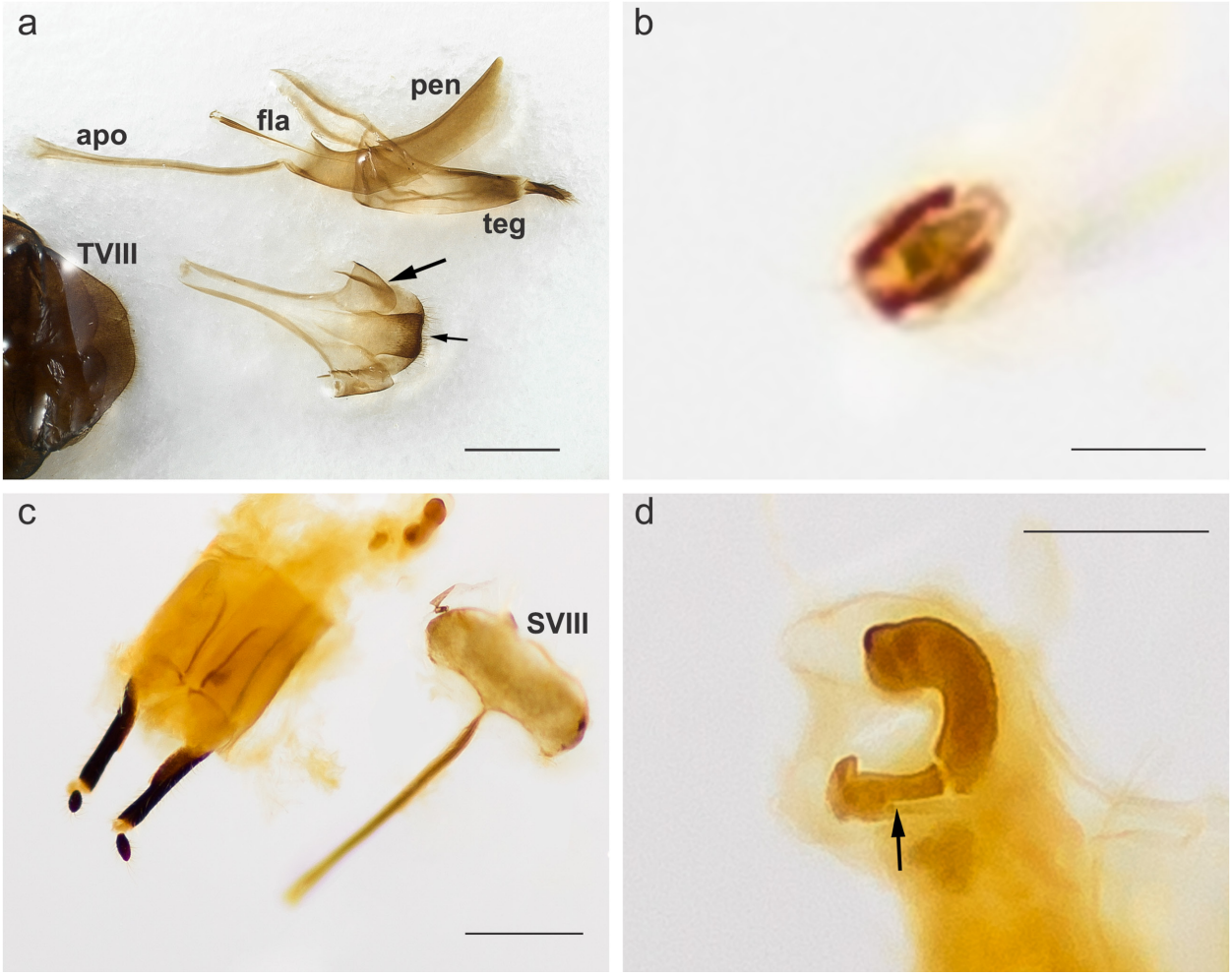

Figure 5. ***Erotylina leoparda*** **(Lacordaire, 1842), male (a–b) and female (c–d) terminalia. a. apophyses (apo), flagellum (fla), penis (pen), tegmen (teg), tergite VIII (TVIII), big arrow showing outer anterior contours of laterotergite IX, small arrow showing posterior edge of sternite IX. b. Head of penile flagellum. c. Female genitalia and sternite VIII (SVIII). d. Spermatheca, arrow showing distal portion of spermathecal duct. Scale bars: a, c = 1 mm; b = 0.1 mm; d = 0.5 mm.**

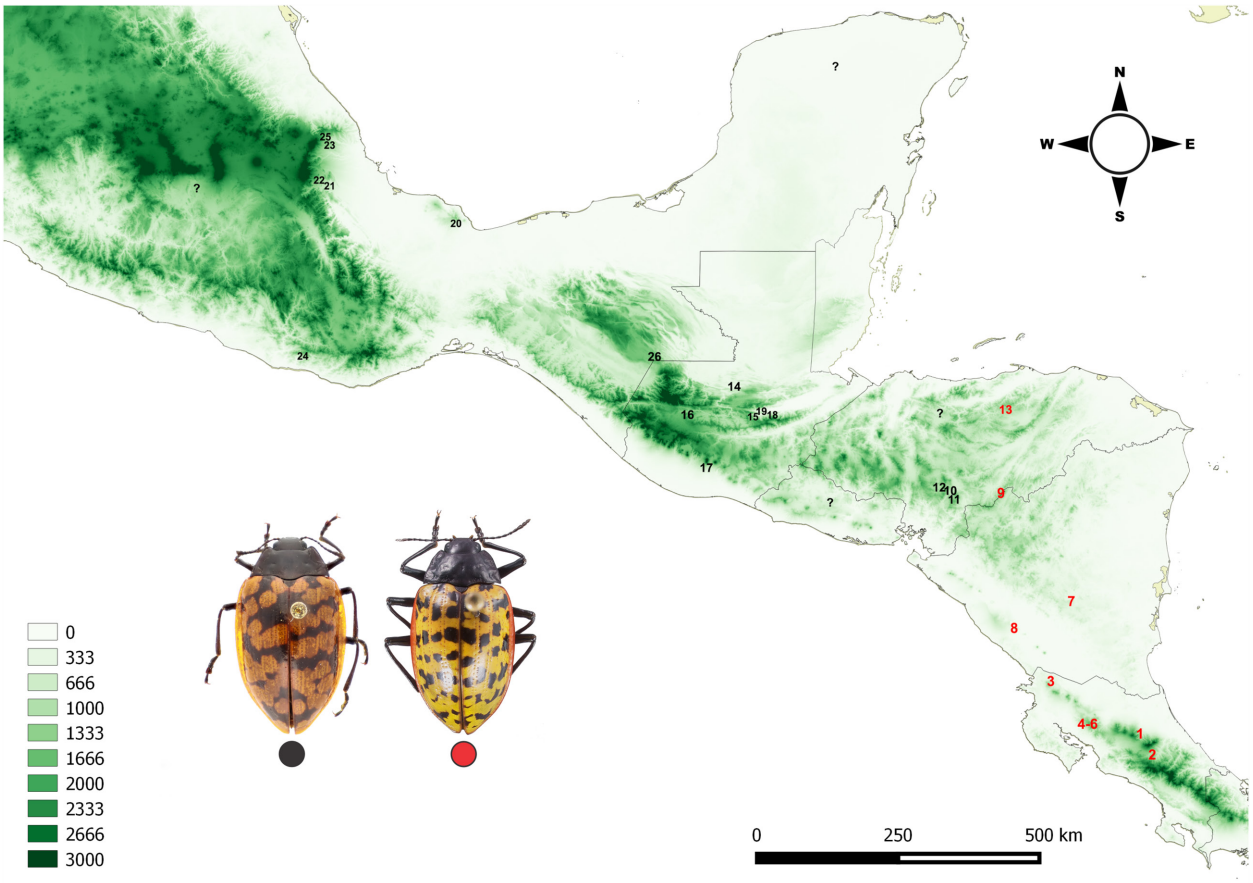

Figure 6. Geographical distribution of *Erotylina leoparda* (Lacordaire, 1842), at different altitude intervals (m). Numbers indicate localities listed in Table I and question marks indicate inaccurate records. Red numbers correspond to variation *nicaraguae* and black numbers to variation *leoparda*.

diagnosis; upper pronotal surface with more or less conspicuous depressions (Figure 2i); mouthparts blackish with maxillary, labial palps and labrum somewhat reddish-brown; apical labial and maxillary setae conspicuously yellowish (Figure 4b), mentum with plate subtriangular (Figure 4b, big arrow), anterior edge convex; antennae blackish.

Head. Glabrous; punctation fine, sparse at disc and coarse on epistome (Figure 4a); epistome slightly constricted, but covering antennal insertions; frontoclypeal suture distinct and not interrupted at middle; ocular striae conspicuous and connected to frontoclypeal suture; single pore on margin, lateral of the ocular striae in front of eyes. Clypeus slightly emarginate, without clypeal marginal bead. Antenna: antennomere I large, elongate, length = 0.7 × antennomere III; antennomere II oval, length = 0.4 × antennomere III; antennomere III elongate, length 1.44 × antennomere I; antennomeres IV to VII elongate, apically rounded, combined length = 1.25 × antennal club; antennomere VIII subtriangular, densely pubescent; antennomeres IX to XI form a loose elongate club, length = 0.79 × antennomeres IV to VII combined; club antennomeres symmetrical. Eyes glabrous (GW 0.84), finely granulate. Mouthparts (Figure 4b–c): Labrum free, sclerotized, pubescent; apex slightly emarginate at middle. Mandibles short, broad (Figure 4c, man); outer apical edge containing setae; apex with two teeth;

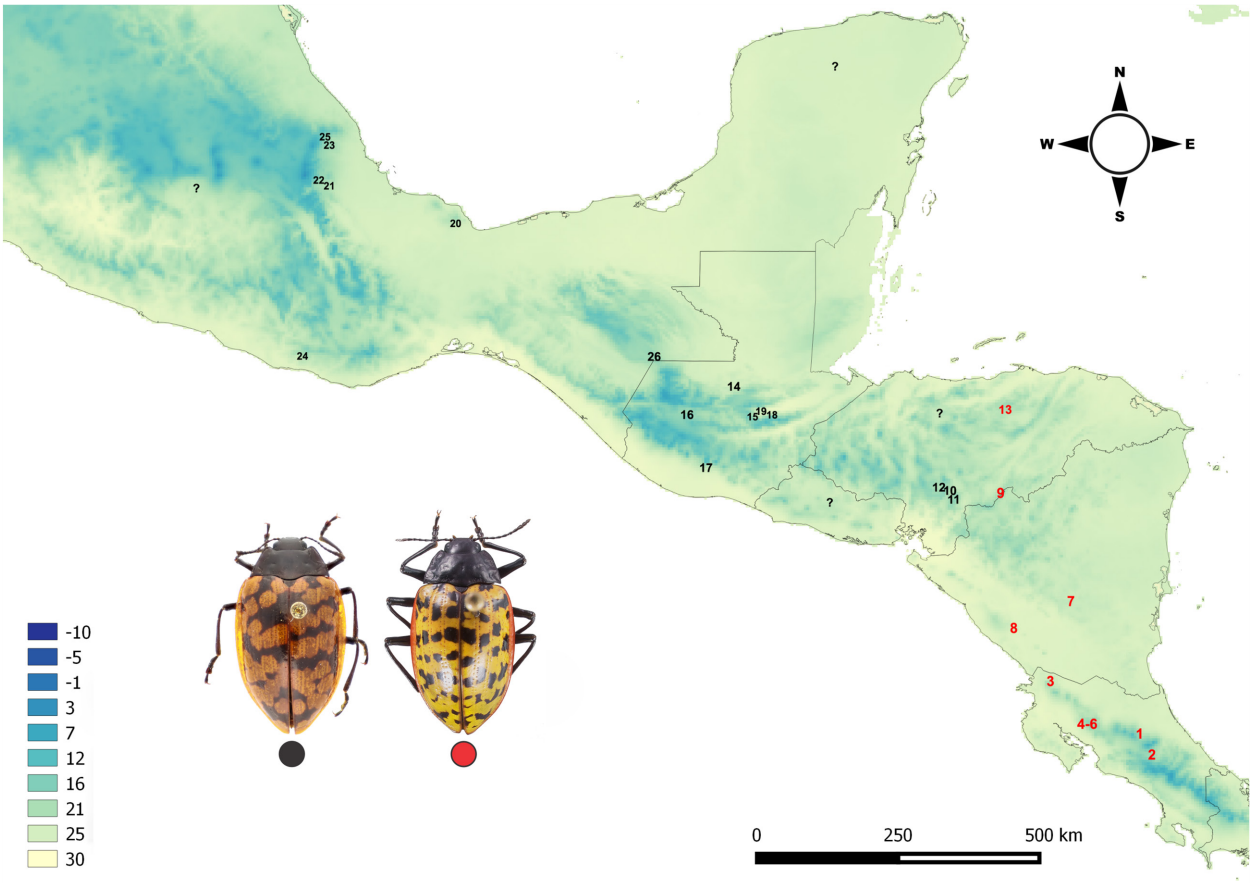

Figure 7. Geographical distribution of *Erotylina leoparda* (Lacordaire, 1842), at different temperature intervals (Cº). Numbers indicate localities listed in Table I and question marks indicate inaccurate records. Red numbers correspond to variation *nicaraguae* and black numbers to variation *leoparda*.

mandibular base emarginate, with additional outgrowth above mola; prostheca distal to mola, soft, with additional tuft of setae. Maxillae with cardo bone-shaped (Figure 4c, car), stipes subtriangular, galea shorter but wider than lacinia, somewhat widened towards densely pubescent apex; lacinia much longer and narrower than galea, densely pubescent at apex, with highly sclerotized and conspicuous pair of hooks (Figure 4c, arrow); maxillary palp with four palpomeres, palpomere I almost as long as palpomeres II–III combined; apical palpomere semicircular (Figure 4b–c, mp), somewhat ovate, approximately 2.34× wider than long and 2.07× wider than apical labial palpomere. Three labial palpomeres on each palp, palpomere III ovate, transverse (Figure 4b, small arrow); mentum subtriangular, anterior edge slightly convex (Figure 4b, big arrow). Subgenal braces (Figure 4b') weakly developed, with a single medial pore; anterior edge slightly sinuous, mandibular condyle visible; lateral edge shallowly rounded, outer contour posteriorly divergent (Figure 4b', black outer contour "diverging" from the red dashed line).

Thorax. Pronotum subtrapezoidal, anterior and lateral edges conspicuously bordered, posterior edge with no marginal bead; pronotal pores numerous along the lateral margins; upper surface with more or less conspicuous depressions (Figure 2i); sides convergent anteriorly in both sexes (in one male and one

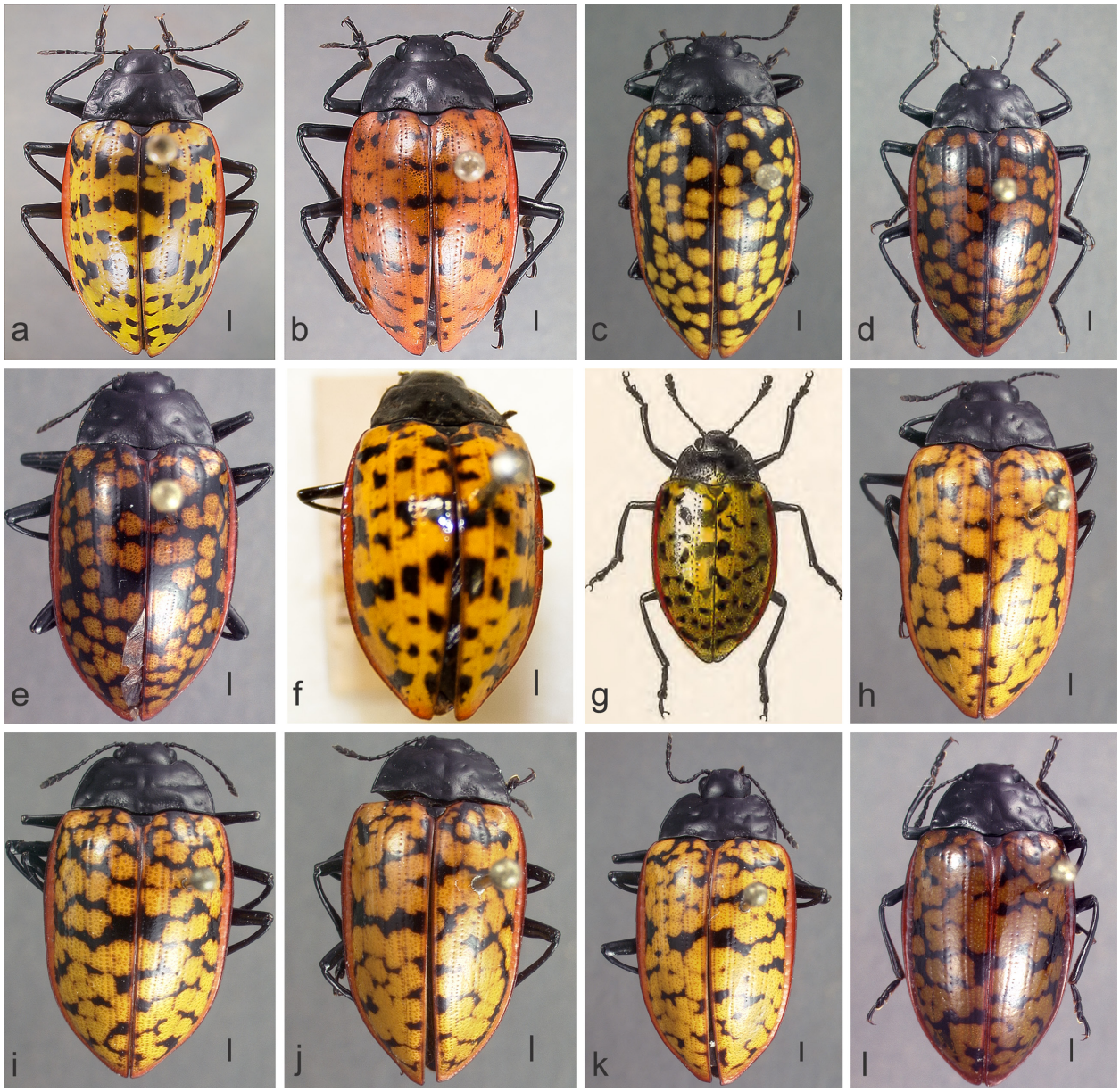

Figure 8. ***Erotylina leoparda*** **(Lacordaire, 1842), morph "*nicaraguae*", specimens from different localities. Numbers in parentheses indicate localities listed in Table I. a–e. Specimens from Costa Rica: a (1), b (3), c (4), d (5), e (6). f–l. Specimens from Nicaragua: f–g (7), h–k (8), l (9). f. Lectotype of *E. nicaraguae* from Santo Domingo (Chontales, Nicaragua). g. Specimen illustrated in Biologia Centrali-Americana (Gorham 1888). Scale bars = 1 mm.**

female examined, the pronotal sides were conspicuously arched in the male and feebly arched (almost straight) in the female). PW/PL = 2.35, widest basally in both sexes; punctation coarse close to basal edge and fine at disc, single, interspaces microreticulate; punctures separated by about 1.76 puncture-widths at disc; anterior edge concave, anterior angles sharp. Scutellar shield BW 0.89 mm, subpentagonal, nearly rounded laterally, glabrous, shiny. Elytra with no anterior marginal bead and sides evenly arched to apex (conspicuously arched at 3/4 of elytra); EL/EW = 1.32 EL/PL = 4.59; with 5–6 striae evident by rows of distinct punctures,

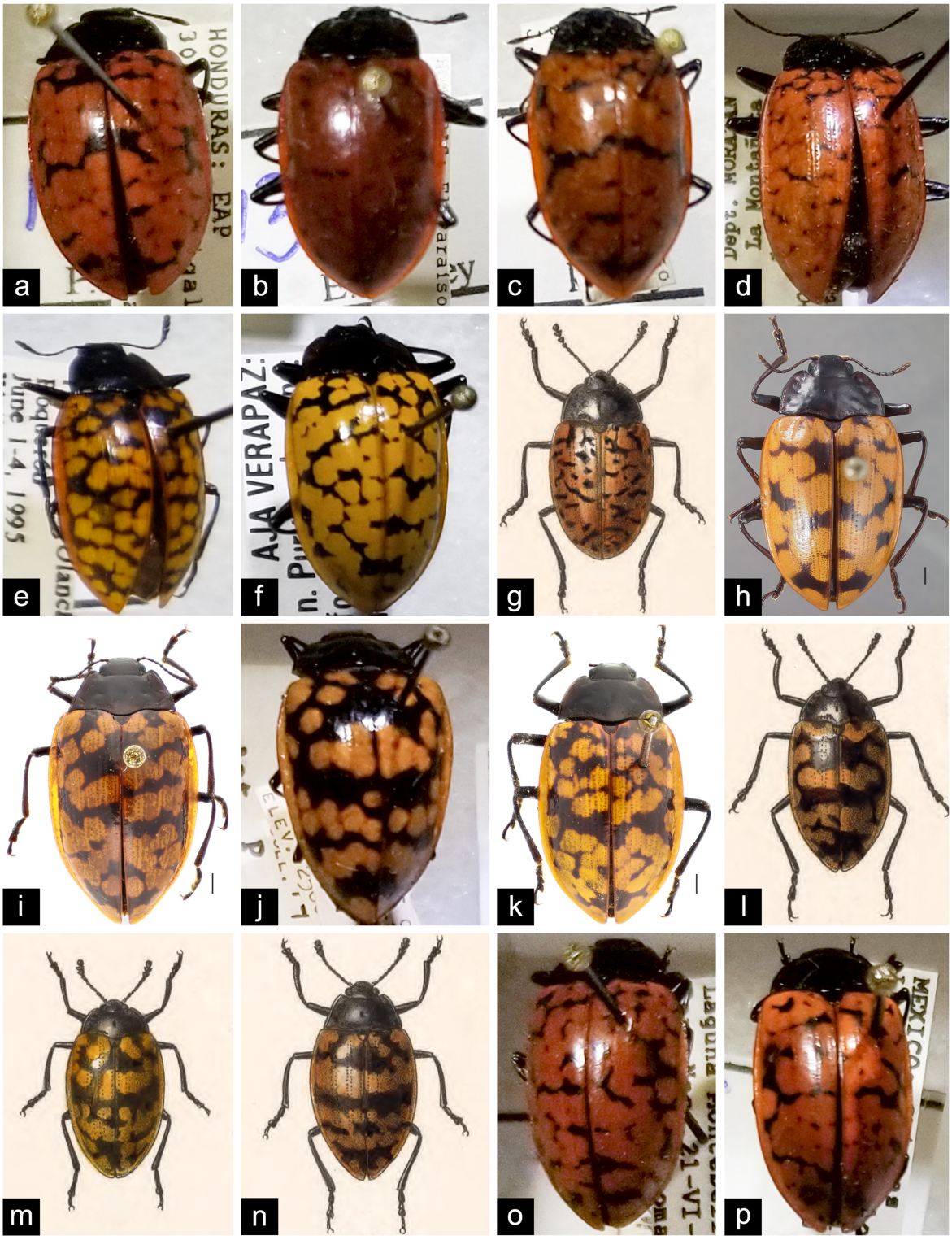

Figure 9. *Erotylina leoparda* (Lacordaire, 1842), specimens from different localities. Numbers in parentheses indicate localities listed in Table I. a–e. Specimens from Honduras (a–d, morph "*leoparda*"; e, morph "*nicaraguae*"): a (10), b–c (11), d (12), e (13). f–g. Specimens from Guatemala: f–g (19). h–p. Specimens from Mexico: h (20), i (21), j (22), k–n (23), o–p (26). g, i–n. Specimens illustrated in Biologia Centrali-Americana (Gorham 1888). Scale bars = h–i, k = 1 mm.

reaching or almost touching elytral base, geminate, as follows: stria I close to mesal sutural elytral edge, striae II–III close to each other and slightly far from stria I, striae IV–V close to each other and far from striae II–III and stria VI not reaching elytral base; interspaces between rows with large, sparse punctures; rows of punctures uniformly longitudinal and not confluent. Metathoracic wings developed, apparently functional (Figure 4d). Outer margin of metascutellum not touching posterior margin of metascutum (Figure 4e, arrows). Prosternum convex; anterior edge smooth or weakly pinched, pubescent; notosternal sutures distinct, entire; procoxal cavities ovate; prosternal process with two basal pores, laterally margined, weakly expanded or more or less straight apically, basal edge shallowly medially emarginate; procoxal lines barely visible and weakly converging anteriorly. Mesoventrite subrectangular, length = 0.76 × distance between mesocoxae; anterior and posterior edges weakly convex; mesocoxal lines straight and weakly arched anteriorly. Metaventrite convex, shiny, with few sparse minute setae; metacoxal lines short, weakly extending laterally; discrimen reaching anterior metaventral edge. Metendosternite well-developed, sclerotized; laminae absent; anterior tendons thin, moderately separated at anterior metendosternal portion (Figure 4f). Legs: Procoxae oval; mesocoxae almost globular; metacoxae transverse, cigarette-shaped. Femora elongate, smooth, without spines or other outgrowths. Tibiae thin, smooth, lacking longitudinal carinae (Figure 4g; present in *Erotylus* Figure 4h, arrow showing the medial carina in a specimen of *Erotylus giganteus*); apex with crown of wide flat setulae and a pair of spurs. Tarsi densely pubescent, protarsomeres I–III approximately of equal length, meso- and metatarsomeres with tarsomere I with length = next two combined.

Abdomen. Slightly elongate; punctation fine with only few gross and sparsely punctures; interspaces microreticulate; vestiture of sparse, slender setae. Coxal lines inconspicuous, continuous around metacoxae, not extending onto disc; sexual dimorphism in males bearing a patch of setae in center of abdominal ventrite I (Figure 4i, arrow). Ventrite 1 elongate, length = 1.56 × ventrite 2; ventrite 2, length = ventrite 5; ventrite 3, length = ventrite 4. **Male terminalia** (Figure 5a–b): penis (Figure 5a, pen) elongate, slightly curved; with weak apical elongation, basal portion with short sclerotized projection linked to the apophyses; internal sac with well-developed flagellum (Figure 5a, fla), approximately as long as penis, with virga swollen close to flagellar head and thin medially and apically; flagellar head U-shaped or horseshoe-shaped (Figure 5b). Apophyses (Figure 5a, apo), approximately as long as penis. Tegmen sclerotized (Figure 5a, teg); parameres sclerotized, with densely pubescent outgrowths. Tergite VIII sclerotized, with sparsely distributed bristles (Figure 5a, TVIII). Sternite VIII slightly sclerotized and medially emarginate. Laterotergite IX sclerotized, pubescent, posteriorly elongate, slightly narrowed; outer anterior contours parabolically rounded (Figure 5a, big arrow); anteroventral edge with paired, feebly arched and subparallel lateral struts, connected at their anterior tips by small, transverse, slightly sclerotized sclerite. Posterior edge of sternite IX conspicuously sclerotized (Figure 5a, small arrow); outer contour rounded; weakly membranous anteriorly. Tergite X sclerotized, U-shaped, posterior edge slightly emarginate, with sparsely distributed bristles. **Female terminalia:** genitalia (Figure 5c–d) with gonostyli and gonocoxites strongly sclerotized; vaginal process laminar and extended to the middle of gonocoxite; baculi of paraprocts sclerotized, slightly arcuate; spermatheca sclerotized, elongate, bean shaped

(Figure 5d); distal portion of spermathecal duct strongly sclerotized, approximate length = 0.5 × the length of spermatheca (Figure 5d, arrow). Tergite VIII sclerotized, with sparsely distributed bristles. Sternite VIII with conspicuous median strut (Figure 5c, SVIII).

Remarks.

1) *Synonymy*: Despite their color variations, the morphology of the dorsum, venter and the components of the male abdominal terminalia are the same and, therefore, we synonymize *E. nicaraguae* with *E. leoparda* in the present work.

2) *Hypothesis of synonymy for future verification*: The following *Erotylina* species, similar to *E. leoparda*, were not synonymized here because more materials needed to be examined: *Erotylina herpestes* (Lacordaire, 1842) has an elytral color pattern similar to the type specimen of *E. nicaraguae*. The main differences are the elytral spots more irregular in *E. herpestes* (one specimen examined, from Colombia, UMCZ). *Erotylina imperfecta* (Crotch, 1876) is known only by its primary type (from Ecuador, UMCZ), an "imperfect" specimen lacking prothorax and head. Although, it has the elytral spots somewhat circular and confluent, similar to those observed in *E. leoparda*, the spots are orange to reddish, also resembling some South American species of *Erotylina*.

3) *Lectotype of E. leoparda*: in the description of *E. leoparda*, Lacordaire (1842) stated the following: "(...) Mes exemplaires ont été recueillis dans le Yucatan par M. Ghiesbreght, jeune naturaliste belge. J'en ai reçu d'autres en communication de MM. Dupont et Reiche." Currently, most Erotylidae specimens studied by Lacordaire are housed in the MNHN, MRSN and UMCZ. We have studied specimens from these three museums. In the Brême collection (MRSN), we found a single unlabeled specimen in the drawer "15" outside written: "Erotyliens – Vrais, 26-28". In the Crotch collection (UMZC), there is a specimen with a label with the word "Type" crossed out. According to Skelley (1998b), labels with the word "Type." crossed out were placed by Crotch indicating that the specimen is probably not the type. The last probable repository is the MNHN. Many of the Lacordaire syntypes are from Dupont collection. According to Horn et al. (1990), and confirmed by us, most of the Dupont's specimens are housed in the Oberthür collection, specimens with labels of a standard format and with the word "*type*". We note the following probable events: Dupont collection was formerly bought by George Vandalin Graf Mniszech, then by Edmond Jean-Baptiste Fleutiaux. Fleutiaux sold the erotylids part of his collection which resulted directly or indirectly in the René Oberthür Collection (Jean-hervé Yvinec, pers. obs., Cambefort 2006). Images courtesy of Jean-hervé Yvinec of drawers from Oberthür collection were examined (Figure 1a–c). The specimen designated as the *E. leoparda* lectotype (Figure 1c) has the first label with the word "Type" indicating that it is a Dupont specimen, one of those examined by Lacordaire (1842).

4) *Lectotypes labels*: It was not possible to put a red label on specimens selected as lectotypes before publication. They will be sent to the appropriate curator of the institutions to be placed on specimens.

5) *Paralectotype of E. nicaraguae*: In addition to the specimen from UMCZ, there is a syntype of *E. nicaraguae* in the BMNH. This specimen has a disc-shaped label with the word "Type". Because the specimen from UMCZ was designated as the lectotype, that one from BMNH is regarded as a paralectotype.

Host fungi. Host fungi information is unknown. To our knowledge, there is a single record of *E. leoparda* on the fungus *Poria* sp.

(Polyporaceae) (Delgado & Navarrete-Heredia 2011).

Distribution. Mexico and Central America (Figures 6–7).

DISCUSSION

Species groups in *Erotylina Curran*

A systematic study about *Erotylina* is ongoing. Based on the material already examined, *E. leoparda* belongs to a species complex readily distinguished from the others by the elytral color pattern with many circular spots and the flagellar head of the penile flagellum horseshoe-shaped. The main differences among these species are the arrangement and coloration of the elytral spots; structurally (dorsum, venter, male and female abdominal terminalia) they are similar to *E. leoparda*. Examples are the following: (i) species with black pronotum and red circular elytral spots which includes *Erotylina geminata* (Crotch, 1876), *E. connectens* (Crotch, 1876), *E. multiguttata* (Lacordaire, 1842), *E. jaspidea* (Erichson, 1847); (ii) species with black pronotum and yellow, free, circular elytral spots which includes *Erotylina intermedia* (Crotch, 1876), *E. scutellata* (Kuhnt, 1908); (iii) species with black circular and transverse pronotal marks, arranged more or less symmetrically, and orange to reddish-brown circular elytral spots which includes *Erotylina flavangula* (Crotch, 1876), *E. atrotibialis* Alvarenga, 1976, *E. dura* Curran, 1944; (iv) species with black pronotum; elytral first half with yellow spots and second half with red spots which includes *Erotylina dichromostigma* (Guérin-Méneville, 1841). Many of these species may be synonymized in future works, when a more complete taxa sampling is examined.

Other *Erotylina* representatives are remarkably different from the *E. leoparda* and its related species, as follows: *Erotylina* sp. (similar to *E. maculiventris* (Lacordaire, 1842)), with black, transverse and sparsely elytral marks and the flagellar head nearly circular with a narrowed tip; *Erotylina gemmata* (Fabricius, 1792), with the elytra conspicuously convex (resembling species of *Cypherotylus* Crotch, 1873 and some *Erotylus*), outer contour of the subgenal braces, posteriorly, only weakly divergent and lateral borders of the flagellar head conspicuously divergent; *Erotylina buqueti* (Lacordaire, 1842), with the elytra yellow, with three serrated black bands and flagellar head posteriorly angulated; *Erotylina helopioides* (Duponchel, 1825), similar to *Erotylus*; body elongate, black with yellow elytral serrated bands; virga of penile flagellum thick and distal portion of the spermathecal duct approximately with the length of the spermatheca. Despite their morphological differences, *E. leoparda* and all *Erotylina* specimens discussed here have the generic diagnostic character "tibiae lacking longitudinal carinae", proposed by Curran (1944). That character, which seems to be a potential apomorphy of this genus, will be examined in future phylogenetic works, with more complete character sampling together with characters proposed in the previous phylogenetic studies on Erotylidae (Węgrzynowicz 2002, Leschen 2003).

Color patterns

Several questions remain on color diversity in the Erotylidae. For instance, the correlation between certain color patterns with host preference and/or feeding habits (Robertson et al. 2004), the mimicry complexes between erotylids and other fungivorous beetles (e.g. Tenebrionidae) and the nature of morph determination if either genetically determined (polymorphism) or plastic (polyphenism) (see examples in other insects in Gullan & Cranston 2014, Ando & Niimi 2018, Briolat et al. 2019). Moreover, some *Erotylina* specimens not treated in this study have a black

pronotum but, at closer examination, we note presence of weak black marks (similar to those described for "group iii" above) that suggests they may be teneral as discussed for Ciidae beetles (Tenebrionoidea) (Pecci-Maddalena & Lopes-Andrade 2017).

Evidence for geographical clines of temperature variations underlying color determination are well documented for insects (Miskimen 1972, Trullas et al. 2007, De Souza et al. 2017, Pecci-Maddalena & Lopes-Andrade 2017, Briolat et al. 2019). Our results revealed two discrete morphs ("*leoparda*" and "*nicaraguae*") distributed across a latitudinal gradient (Figures 6–7), with intermediate and continuous color variations distributed across altitudinal and temperature gradients (Figures 8–9, Table I). In each morph are specimens (variations) with more discrete elytral spots and darker elytra that are usually collected in higher altitudes and lower temperatures (Table I). These provide evidence of a temperature-dependent polyphenism or a melanism related with thermoregulation (see Trullas et al. 2007, definition of the "thermal melanism hypothesis" and Figure 3, present work). Interestingly, some *E. leoparda* specimens, available at www.inaturalist.org, confirm the color gradient described here, as follows: for the "*leoparda*" morph, see a specimen from "Villaflores, Chiapas, Mexico", ~570 m, with elytral spots almost completely fused and the specimens from "Rancho El sinaí, Jilotepec, Veracruz, Mexico", ~1500 m, with more discrete elytral spots and darker elytra. For the "*nicaraguae*" morph, see a specimen from "Granada, Nicaragua", ~60 m, with elytral spots most fused and a specimen from "Sabana Redonda, Costa Rica", ~1500 m, with more discrete elytral spots and darker elytra.

Exceptions to these geographical patterns are rare and deserve examination. The specimens from "Lagunas de Montebello National Park (Chiapas, Mexico)" at high altitude (1524m) have the elytral spots mostly fused. However, in this area the average monthly temperature (23.6°C) is warmer than other localities (Table I). It is possible the local temperature increase has some effect on the pigmentation of these specimens. In another example, a specimen collected close to Purulhá (Baja Verapaz, Guatemala), a locality (Table I) at a high altitude (1524m) and low average temperature (16.9°C) also has the color pattern similar to the previous specimen. In this case, it is possible the specimen developed at a locality with different environmental conditions and dispersed to Purulhá. Based on metathoracic wing development (Figure 4d), the occurrence of broadly distributed species (Skelley 1998a, Pecci-Maddalena & Lopes-Andrade 2018b) and our field observations, most erotylids are probably good flyers and capable of traveling long distances. Even with these occasional records, the geographical distribution of *E. leoparda* and its phenotypic variations denote a well-defined pattern. Further research employing rigorous experimental testing is needed to confirm the effects of different temperatures and other environmental variables on the coloration of any member of the Erotylidae. For now, we provide a starting point for discussion and further research.

The Mexican transition zone (MTZ), corresponding to mountainous areas of central and southern Mexico and northern Central America (Morrone 2014), is a major corridor/barrier that has driven the geographic distribution of several taxa, from plants to insects (Nolasco-Soto et al. 2017). The geographical records of the "*leoparda*" and "*nicaraguae*" morphs reveal that they occur across the MTZ and overlap in a narrow contact zone in northern Nicaragua and northern Honduras (Figures 6–7). In this context, intraspecific phylogeographic analyses as those performed for other taxa from the

MTZ (Nolasco-Soto et al. 2017, Morrone 2020), including DNA analyses of various populations with an examination of genetic distance, are required to verify if the "*leoparda*" and "*nicaraguae*" morphs are monophyletic lineages or represent a single species as suggested here by the morphological data.

CONCLUSION

The characters described here for *E. leoparda* (mouthparts, thorax, male and female abdominal terminalia, etc.), the new geographical records and the discussion of potential species groups of *Erotylina*, shed light on its taxonomy and are interesting topics for future systematic studies. Additionally, the present study provides the first clear evidence of a relation between geographical distribution, altitude, latitude and temperature in Erotylidae. A hypothesis for future verification is if the *E. leoparda* complex corresponds to a few species or a single species under a spectrum of phenotypes, distributed across a latitudinal, longitudinal and/or temperature gradients. Another question is, under a gradient of biotic change and genetic possibilities, how the color patterns evolved in *Erotylina*.

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