



Giant water scavenger beetles *Hydrophilus* subgenus *Dibolocelus* (Coleoptera: Hydrophilidae) from Mexico with description of two new species

ROBERTO ARCE-PÉREZ¹, EMMANUEL ARRIAGA-VARELA^{2*}, RODOLFO NOVELO-GUTIÉRREZ¹ & JOSÉ L. NAVARRETE-HEREDIA²

¹Instituto de Ecología, A.C., Red de Biodiversidad y Sistemática, Carretera Antigua a Coatepec, 351, El Haya, 91070, Xalapa, Veracruz, Mexico.

✉ roberto.arce@inecol.mx; <https://orcid.org/0000-0002-7714-6943>

✉ rodolfo.novelo@inecol.mx; <https://orcid.org/0000-0003-3163-2820>

²Centro de Estudios en Zoología, CUCBA, Universidad de Guadalajara, Apdo. postal 134, Zapopan, Jalisco, Mexico.

✉ glenusmx@gmail.com; <https://orcid.org/0000-0002-3336-8528>

*Corresponding author. ✉ arriagavarelae@gmail.com; <https://orcid.org/0000-0001-6206-9212>

Abstract

The *Hydrophilus* (*Dibolocelus*) Bedel species from Mexico and adjacent areas are treated on the basis of the study of 142 adult specimens and published data. Two new species are herein recognized and described: *H. (D.) nucleoensis* Arce-Pérez & Arriaga-Varela **sp. nov.** from Mexico, Guatemala and Nicaragua, *H. (D.) pseudovatus* Arce-Pérez & Arriaga-Varela **sp. nov.** from Mexico. Three already known species are re-described and their geographical distribution is updated, *H. (D.) ovatus* Gemminger & Harold and *H. (D.) pollens* Sharp and *H. (D.) violaceonitens* Jacquelin du Val, a species resurrected as distinct to *H. (D.) smaragdinus*. *Hydrophilus (D.)* cf. *purpurascens* (Régimbart) is also redescribed but their identity is questionable. The lectotype of *H. (D.) pollens* Sharp is designated. Within Mexico, the state with the highest known diversity is Veracruz with five species. A key to the species of *Hydrophilus (Dibolocelus)* from Mexico and Central America is provided.

Key words: Aquatic beetles, Neotropical region, new taxa, status restored, morphology, distribution

Introduction

The genus *Hydrophilus* Geoffroy, 1762 is a group of distinctly large aquatic beetles, with saprophagous or facultative phytophagous habits (Martin Fikáček, personal communication). It is currently composed of 50 species worldwide, classified in three subgenera: *Hydrophilus (sensu stricto)* Geoffroy, 1762, *Dibolocelus* Bedel, 1891 and *Temnopterus* Solier, 1834 (Hansen 1999; Toussaint et al. 2017). The first two are represented in the New World by 19 species: one is found exclusively in the Nearctic, 16 in the Neotropics, and two have their distribution range throughout both zoogeographic regions (Hansen 1999, Short & McIntosh 2014, 2015). Hansen's (1991) placement of *Dibolocelus* as a subgenus within *Hydrophilus* rather than a distinct genus was recently tested and supported by Short (2010) through a morphological phylogenetic analysis of the tribe Hydrophilini that included the study of *Hydrophilus* species from North and Central America. A molecular phylogeny of tribe Hydrophilini (Toussaint et al. 2017) supported the monophyly of *Dibolocelus*; however, it seemed to suggest that its inclusion would render *Hydrophilus sensu stricto* a paraphyletic group. Additional taxonomical sampling is needed in order to have a clear insight of the subgeneric relationships within *Hydrophilus*. Arce-Pérez & Morón (2013) reviewed the *Hydrophilus s.str.* species from Mexico and Central America, updating the known distribution of the species, while Short & McIntosh (2014) reviewed the *Hydrophilus* species of the United States of America and Canada, updating their distribution and providing new records from Mexico.

Currently, a total of 10 species of *Hydrophilus (Dibolocelus)* are known (Hansen 1999; Short & McIntosh 2014, 2015), one of them is distributed in the Nearctic Region and the remaining nine restricted to the Neotropics. *Dibolocelus* specimens are not abundant in most of the entomological collections of Mexico and Central America. This situation has led to a scarcity of information about their distribution in the region and uncertainty about the

presence of certain species. So far, four species are recorded from the area: *H. (D.) smaragdinus* Brullé, 1837, *H. (D.) pollens* Sharp, 1887, *H. (D.) purpurascens* (Régimbart, 1901) and *H. (D.) ovatus* Gemminger & Harold, 1868 (Hansen 1999; Arce-Pérez & Morón 2013; Short & McIntosh 2014). In this contribution, we update the information about the diversity of this subgenus in Mexico based on the study of specimens deposited in several entomological collections of the country and other Central American countries. The type of *H. (D.) pollens* deposited in the Museum of Natural History, London, UK, was also examined. We describe two new species and re-describe the known species from the region. An illustrated key for the identification of the known species of the subgenus in Mexico and Central America, and updated distribution maps are provided.

Material and methods

The present contribution is based on the study of 138 specimens of *Hydrophilus (Dibolocelus)* deposited in the following entomological collections:

AOBC	A. O. Bachmann personal Collection, Argentina (Axel O. Bachmann);
BMNH	The Natural History Museum, London, United Kingdom (Christine Taylor, Maxwell Barclay);
CNIN	Colección Nacional de Insectos, Universidad Nacional Autónoma de México, Mexico City, Mexico (Santiago Zaragoza-Caballero);
CZUG	Centro de Estudios en Zoología, Universidad de Guadalajara, Zapopan, Mexico (José L. Navarrete-Heredia);
INBIO	Instituto Nacional para la Biodiversidad, Costa Rica (Ángel Solís);
IEXA	Colección Entomológica, Instituto de Ecología, A.C. Xalapa, Mexico (Roberto Arce-Pérez);
INIFAP	Colección Instituto Nacional de Investigaciones Forestales, Agrícolas y Pecuarias, Celaya, Mexico (Antonio Marín Jarillo);
MNHN	Muséum National d'Histoire Naturelle, Paris, France (Antoine Mantilleri);
NMPC	National Museum, Prague, Czech Republic (Martin Fikáček);
SEMC	University of Kansas, Lawrence, Kansas, USA (Andrew E.Z. Short);
UVGC	Colección Entomológica, Universidad del Valle de Guatemala, Guatemala, Guatemala (Enio Cano).

The specimens were studied with a Carl Zeiss IV-B or an Olympus SZX 16 stereomicroscope. The microphotographs were taken with a Nikon DS-U3 camera attached to a Nikon SMZ25 stereomicroscope and a Canon EOS 1100D digital camera attached to an Olympus BX41 compound microscope. Habitus photographs were taken using a Canon EOS 550D digital camera with a Canon MP-E65mm f/2.8 1–5× macro lens attached or a Nikon Coolpix P500. The photographs were later processed in Adobe Photoshop CS5 program. Descriptions are based on male specimens and comments on the sexual dimorphism and interspecific variation are provided. Measurements are in millimetres. Geographical coordinates were obtained in Google Earth (<https://www.google.com/earth>) and provided in brackets, when they were not part of the original label data in the list of studied material. The maps were generated on SimpleMappr (<https://www.simplemappr.net/#tabs=0>) and edited with Corel Draw.

Results

Taxonomy

Hydrophilus (Dibolocelus) Bedel, 1891

Dibolocelus Bedel, 1891: 309.

Type species: *Hydrophilus palpalis* Brullé, 1837.

Diagnosis. In addition to the characters for the genus (Short 2010), adult *Hydrophilus (Dibolocelus)* can be differen-

tiated from those of *Hydrophilus* (*s. str.*) by a more convex and robust body shape; maxillary palps usually modified being generally longer, broadened and curved towards apex, sometimes inflated and curved at mid-length, with third palpomere with deep and wide ventral excavation or flat and slightly widened towards the apex; labial palp widely triangular and inflated, clavate or subparallel in shape, with or without setae on lateral margins; fifth protarsomere wide and longer than any of the previous ones, sometimes slightly flattened and with a ventral laminar expansion, never as large as those in *Hydrophilus* (*s.str.*); internal spur of anterior tibia flat, sub-rectangular or rounded, with straight or curved external margins, if sub-rectangular then it can be short or long with its apex straight, irregular or clearly bifid; abdominal ventrites 3 and 4 have slight to well-marked oval, glabrous area at mid-line, and ventrite 5 has a wide oblong or sub-triangular glabrous area; ventrites 3 to 5 slightly raised at midline, flattened or forming a keel, slightly projected above ventrite posterior margin.

***Hydrophilus (Dibolocelus) ovatus* Gemminger & Harold, 1868**

Figs. 1, 2; 7–10, 41.

Hydrophilus ovalis Ziegler, 1844: 45 (primary homonym of *Hydrophilus ovalis* Brullé, 1837: 53, and *Hydrophilus ovalis* Castelnau, 1840: 50).

Dibolocelus ovalis (Ziegler); Régimbart, 1901: 225.

Hydrophilus ovatus Gemminger & Harold, 1868: 476 (replacement name for *Hydrophilus ovalis* Ziegler).

Stethoxus ovatus (Gemminger & Harold); Bedel, 1891: 314.

Hydrous (Dibolocelus) ovatus (Gemminger & Harold); Kuwert, 1893: 83.

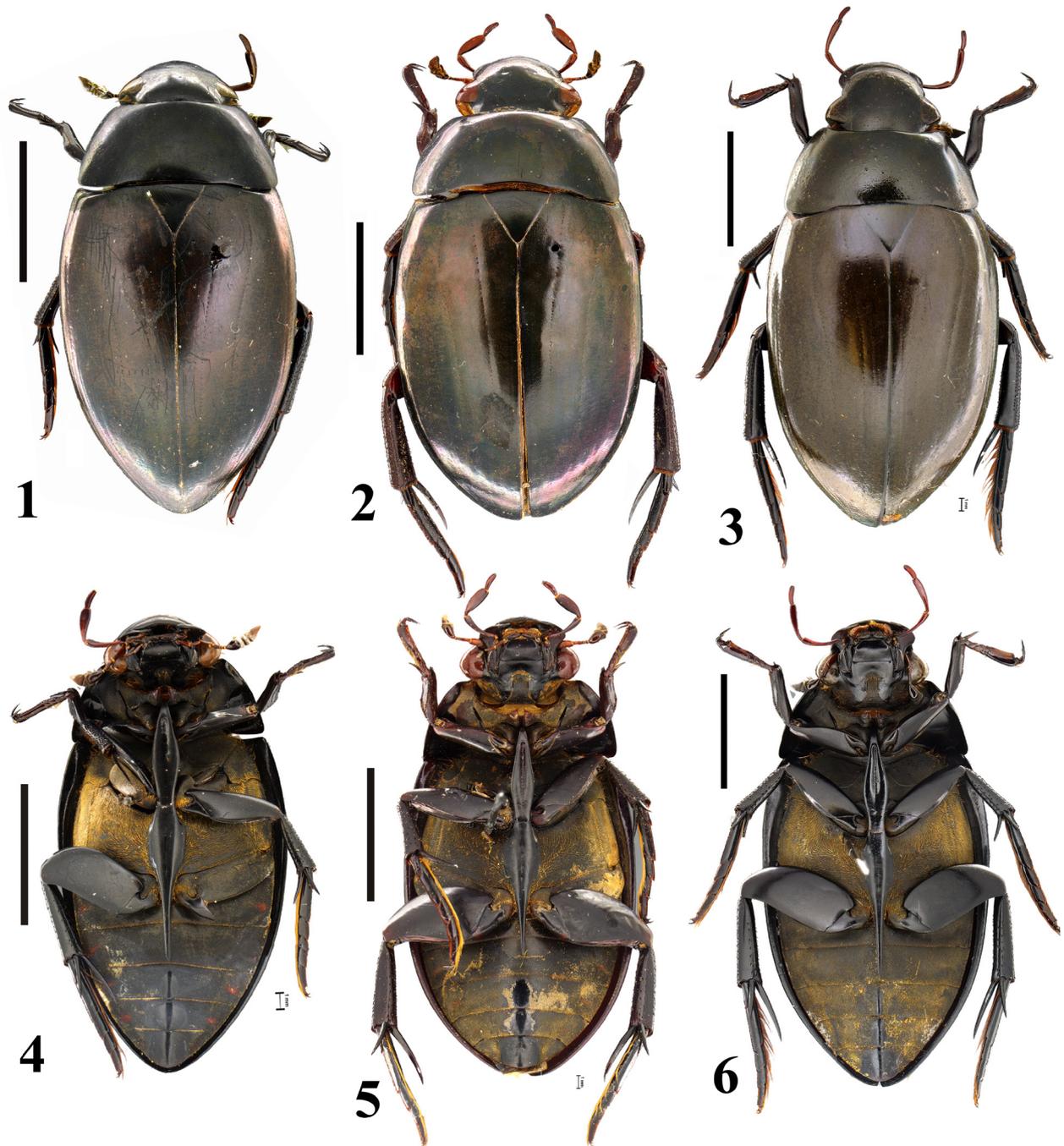
Dibolocelus ovatus (Gemminger & Harold); Young, 1954: 196.

Studied material. United States of America: Louisiana, New Orleans, 26.vii.1959, At light, W. Gibson col. (3 ♂, 2 ♀) [INIFAP].

Diagnosis. This species is distinguished by the following combination of characters: maxillary palpi slender, third palpomere slightly flattened and broadened apically; internal protibial spur sub-rectangular with apex truncated, straight; fifth protarsomere robust, longer than basal ones together. Regarding the characters of body shape, color, vestiture, antenna, maxillary palps and male genitalia, the specimens of *H. (D.) ovatus* from North America, are very similar to those of *H. (D.) pseudovatus* **sp. nov.** from Mexico but can be distinguished by [characters of *H. (D.) pseudovatus* are provided in brackets for comparative purposes characters of *H. (D.) pseudovatus*] third maxillary palpomere slightly flattened and broadened apically, with its internal margin slightly straight, maximum width 0.080 mm (Fig. 7) [third maxillary palpomere markedly flattened and broadened toward the apex, with its internal margin slightly convex(Fig. 11)]; fifth protarsomere longer and robust than the basal ones together (Fig. 8) [fifth protarsomere shorter than basal tarsomeres together, flat and with a slight but evident internal laminar expansion (Fig. 12)]; the metaventral spine reaches or exceeds the posterior margin of the second abdominal ventrite (Figs. 2, 9) [short metaventrite spine, not exceeding 3/4 of the second abdominal ventrite (Figs. 4, 13)]; ventrites 3 and 4 raised, with their apical margin slightly acute and slightly projecting over the next ventrite (Fig. 9) [ventrites 3 and 4 slightly raised, with their apical margin slightly rounded and slightly projecting over the following ventrite (Fig. 13)]; ventrites with evident yellowish-reddish lateral oval spot [ventrites without spots].

Description. Body elongate-fusiform, length 30-33 mm, width 17-18 mm at humeri, 1.7-1.8× longer than wide, dorsally strongly convex and glabrous, ventrally flat and pubescent; body color black with dark greenish tone, ventrally black with red-yellowish hue, vestiture pale yellow; antennae, palpi and legs dark-reddish, the antennal club slightly lighter.

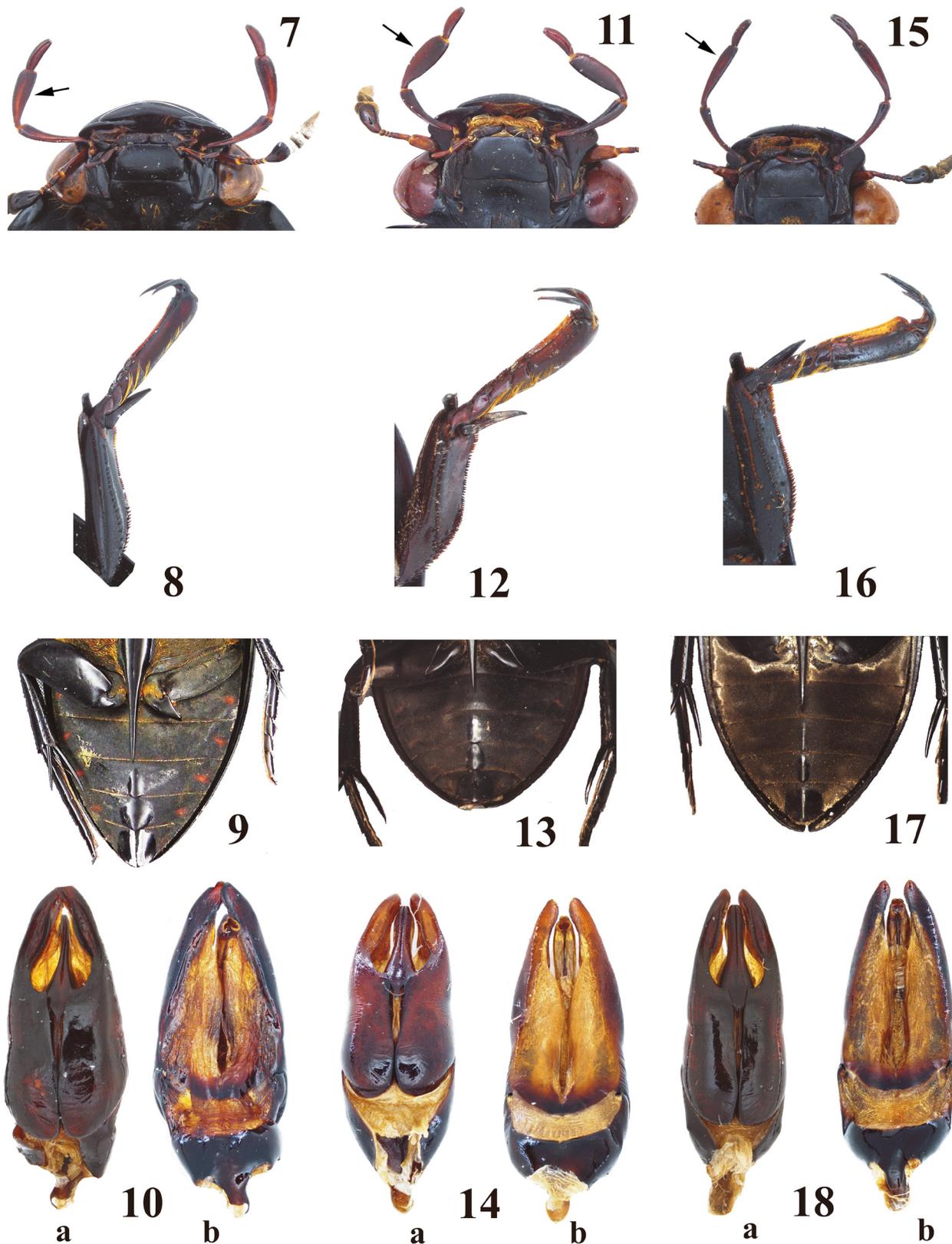
Head: Antenna short, scape large and robust, longer than the next four antennomeres together; pedicel subequal to the next three antennomeres; sixth long and oval with apex rounded, subequal to previous four together, not covering the first antennomere on the club (Fig. 7). Maxillary palpi long and slender, with four palpomeres, with lengths: 0.4, 2.8, 2.66, 1.4 mm; first palpomere small, subconical; second long, curved and slightly broadened towards apex; third shorter, curved, slightly flattened and broadened towards apex, around 0.80 mm in its widest part, fourth short and oval, with apex truncated. Mentum broad, hexagonal, 1.8× wider at base than long, lateral margins parallel at basal half, apically converging straightly, apex truncated and straight; labial palpi short, length of palpomeres: 0.03, 0.08, 0.06 mm; first palpomere small and broad; second long and slightly broadened towards apex, 1.3× longer than the third and with short golden setae at inner margin near apex; third short and oval, with apex rounded (Fig. 7).



FIGURES 1–6. Dorsal and ventral view of *Hydrophilus (Dibolocelus)* spp. 1–2 *H. (D.) ovatus* Gemminger & Harold; 3–4 *H. (D.) pseudovatus* sp. nov.; 5–6 *H. (D.) nucleoensis* sp. nov.

Thorax: Prosternal lobes raised and apically rounded, with short reddish-yellow setae at apex; mesoventrite with keel wide, with lateral margins rounded and convergent towards apex, with a broad and shallow concavity at basal half, deeper near apex; metaventrite with a broad, flat keel with a median longitudinal groove, ending as a long spine reaching the posterior margin of the second abdominal ventrite (Fig. 2). Elytra with four well-marked rows of small black spots, two on the disc, one sublateral starting after the humerus, and another one less complete on each side.

Legs: Anterior tibiae with internal spur short, flat, sub-rectangular with its truncated and straight apex, the longer external spur, acute sub-triangular; fifth protarsomere wide, and longer than the previous ones together. Tarsal claw long, curved and without a tooth in the base, internal claw little longer than the external. Protarsomeres 2–5 with tufts of golden setae in the outer edge (Fig. 8).



FIGURES 7–18. Morphological structures and male genitalia of *Hydrophilus (Dibolocelus)* spp. **7–10** *H. (D.) ovatus* Gemminger & Harold; **7** ventral view of head (arrow: third labial palpomere); **8** protibia and tarsi, **9** ventral view of abdomen; **10a** aedeagus ventral; **10b** aedeagus dorsal; **11–14** *H. (D.) pseudovatus* sp. nov.; **11** ventral view of head (arrow: third labial palpomere); **12** protibia and tarsi, **13** ventral view of abdomen; **14a** aedeagus ventral; **14b** aedeagus dorsal; **15–18** *H. (D.) nucleovatus* sp. nov.; **15** ventral view of head (arrow: third labial palpomere); **16** protibia and tarsi, **17** ventral view of abdomen; **18a** aedeagus ventral; **18b** aedeagus dorsal.

Abdomen: Vestiture leaving a wide, long, oval glabrous area at mid-line in ventrites 3–4; and a broader sub-rectangular one in ventrite 5. Ventrites 3 and 4 raised and flattened above, with apex slightly acute and projected on the next ventrites. All ventrites bearing a yellow-reddish oval spot on each side (Figs 2, 9).

Genitalia: Total length 5.4 mm; phallobase long, (length: 2.7 mm, width: 2 mm), widest at union with parameres, manubrium slender with apex rounded. Parameres long (3.95 mm), very wide at basal 3/5, and elongated oval in their 2/5 apical, with a wide and deep oval concavity not reaching apex, and with minute teeth in the internal margin at the apical half, getting more abundant apically. Median lobe slightly shorter than parameres (3 mm), wide, sub-triangular, with a longitudinal median groove, and apex rounded (Fig. 10 a, b).

Sexual dimorphism. Female specimens are similar to males but with maxillary palpi narrow, tibiae with long sub-triangular spurs, tarsal claws curved and acute, with an acute basal tooth.

Distribution. The reported distribution of this species includes the United States of America, Southern Canada and Mexican states Chiapas, Michoacán, Nayarit, Quintana Roo, San Luis Potosí, Tamaulipas and Veracruz (Smetana 1988; Short & McIntosh 2014) (Fig. 41). Nevertheless, in the present work we found no additional specimens from Mexico among the studied material and the description is based on specimens collected in USA.

Taxonomical comments. Andrew E.Z. Short (SEMC) (personal communication), noticed the existence of specimens from Veracruz of *H. (D.) ovatus* that show a certain degree of intergradation with *H. (D.) pseudovatus* **sp. nov.** in regards to the protarsomeres of males where the articles are slightly flattened, although not completely forming a laminar expansion as in the new species. Extensive additional sampling in Mexico and analysis of the genetic information of these population is needed in order to better elucidate the status of these two species.

Hydrophilus (Dibolocelus) pseudovatus Arce-Pérez & Arriaga-Varela **sp. nov.**

Figs. 3, 4; 11–14, 41.

Etymology. Named *H. (D.) pseudovatus* (ancient Greek *pseudes* = false) in recognition of the external resemblance of this species to *H. (D.) ovatus*.

Type material (25♂, 14♀). **Holotype male:** MEXICO: Nayarit, San Blas, Matanchén, 80 m, 26.vii.2007, 21°30' N, 105°14' Oeste. G. Nogueira col. 1 ♂ (IEXA). **Paratypes.** San Blas 7.xi.1980, [21°32'23"N 105°17'08"O], M. Beltran col. 1 ♂; 6.xii.1980 M. Teresa Ortiz col. 1 ♂; 9.xii.1980, R. Arce col. 2 ♂ (IEXA); San Blas 4.xi.1991, R. Barba y E. Barrera col. 5 ♂ (CNIN), Guerrero, Técpan de Galeana, Papanoa xi.1970, [17°19'28"N 101°02'28"O] J. Hendrichs col. 1 ♂ (CNIN), Técpan de Galeana, Tetitlán, [17°07'00"N 100°28'00"O], 19.xii.1981, V. Reyes col. 1 ♂ (IEXA). Técpan de Galeana, 18.vi.1982, I. Abarca col. 1 ♂ (IEXA). Colima, Tecomán, Tecomán, [18°54'32"N 103°52'29"O], xi.1970, 4♂, 5♀ (INIFAP-Celaya). Jalisco, Tomatlán, presa Cajón de Peñas, La Quebrada, BTC, 100 m, [19°56'3" N, 105°14'8" O], 12.x.1996, J. C. Rodríguez col. 1 ♂ (CZUG); Punta Pérula, [19°36'18" N, 105°9'30" W], 28.x.1999, L. G. Martínez col. 1 ♀ (CZUG); Punta Pérula, [19°37'27.1" N, 105°7'34.4" W], a la luz, 11.xi.1999, H. E. Fierros col. 2 ♂ (CZUG) Chamela, Arroyo, [19°30'38"N 105°03'24"O], 13.x.1991, C. Mayorga y G. Ortega cols. 1 ♂ (CNIN), Est. de Biol. Chamela, A. Pescador col. [19°30'38"N 105°03'24"O], 30.vii.1980 1 ♂ (CNIN). Puebla, San José Acateno, Río Saltero, [20°08'00"N 97°12'00"O], 162 m, 19.vii.1999, G. Hernández col. 1 ♂ (IEXA). Oaxaca, Putla Villa de Guerrero, [17°01'33"N 97°55'45"O] 740 m 12-vii.2013, Julian, H. C. col. 1 ♂ (IEXA). Veracruz, Alto Lucero, 5 km. Norte de Palma Sola, 19°10'51" N Longitud: 96°08'34" O, 22.iv.1990, Luz Mercurial, F. Capistran y L. Delgado Cols. 2 ♀, Los Tuxtles, [18° 35.11' N, 95° 04 O], 130 m, 8.iv.1982, T. Ortiz Col. 1♀, Los Tuxtla, El Vigía, 700 m, 2/12.vii.1972 1♀, Tamiahua, Laguna de Tamiahua, [21°16'46"N, 97°26'49"O], 30.vii.1936, P. Roveglia 1♀, Jalcomulco, Bordes de selva mediana, [19°20'00"N 96°46'00"O], 380 m, 11.vi.2005, Fdo. Escobar col. 1♀, Actopan, La Mancha, 19° 39N, 96° 27'O, 1♀ (IEXA). Morelos, Jojutla, [18°36'53"N 99°10'49"O], 750 m, 1♀? (CNIN).

Diagnosis. The specimens of *H. (D.) pseudovatus* **sp. nov.** are very similar to those of *H. (D.) ovatus* from North America. The new species can be distinguished from *H. (D.) ovatus* because [the characters of *H. (D.) ovatus* are provided in brackets for comparative purposes the characters of *H. (D.) ovatus*] third maxillary palpomere shorter and wider, curved towards apex, markedly flattened and broadened toward the apex, with 0.085 mm in its side wider (Fig. 7) [third maxillary palpomere slightly flattened and broadened towards its apex, with its internal margin slightly convex (near 0.80 mm in its widest part) (Fig. 11)]; the fifth protarsomere shorter than basal tarsomeres together, flat and with a slight but evident internal laminar expansion (Fig. 12) [fifth protarsomere is long

and wide, longer than the basal tarsomeres together, no internal expansion (Fig. 8)]; the metaventral spine shorter, not exceeding 3/4 of the second abdominal ventrite (Figs. 4, 13) [metaventral spine longer, reaches or exceeds the posterior margin of the second abdominal ventrite (Figs. 2, 9)]; ventrites 3 and 4 slightly raised, with their apical margin slightly rounded and very slightly projecting over the following ventrite (Fig. 13) [ventrites 3 and 4 raised, with their apical margin slightly acute and slightly projecting over the next ventrite (Fig. 9)]; abdominal ventrites without evident yellowish-reddish lateral oval spots [ventrites with evident yellowish-reddish lateral oval spots]; median lobe broad (Fig. 14) [narrower in *H. (D.) ovatus* (Fig. 10)].

Description male holotype. Body elongated-fusiform, length 32–36 mm (male holotype: 35 mm), width 17–17.5 mm at humeri (Holotype: 17 mm), 2× longer than wide, dorsally strongly convex and glabrous, ventrally flat and pubescent; dorsal color black with dark green tone; ventrally black with reddish yellowish hue, ventral vestiture pale yellow; antennae, palpi and legs dark-reddish (Figs 3, 4).

Head: Antennae short with nine antennomeres, scape large and robust, longer than the next four antennomeres together, pedicel subequal to the following three antennomeres, sixth antennomeres long and oval, subequal to the previous four together, not covering the first article of antennal club (Fig. 11). Maxillary palpi long and slender, with four palpomeres, with lengths: 0.04, 0.29, 0.27, 0.14 mm; first palpomere small, sub-conical, second long, curved, slightly broadened towards apex, third shorter and wider, curved towards apex, markedly flattened toward the apex, with 0.085 mm in its side wider, fourth short, oval, with truncated. Mentum hexagonal, 1.7× wider at base than long, lateral margins parallel at basal half, apically converging straightly, apex truncated and straight. Labial palpi short, length of palpomeres: 0.02, 0.09, 0.06 mm; first palpomere small and broad, second long and slightly broadened towards apex, 1.5× longer than the third, with short golden setae near the internal margin apex, third palpomere short and oval, with apex rounded (Fig. 11).

Thorax: Prosternal lobes raised and apically rounded, with short reddish-yellow setae at apex; mesoventrite with keel long and narrow, with lateral margins rounded and convergent towards apex, with a broad and shallow concavity at basal 3/5, deeper near apex. Metaventrite with keel wide and flat, with feeble median longitudinal groove, ending as a long spine reaching half-length of the second abdominal ventrite (Fig. 4). Elytra with four well-marked rows of black spots, two on the disc, one sublateral starting after the humerus, and other more incomplete on the sides (Fig. 3).

Legs: Anterior tibiae with two spurs; internal one shortest, flat, sub-rectangular with apex truncate straight, with a small notch close to the external margin; external spur longer, sub-triangular, acute; fifth protarsomere shorter than the previous ones together, broadly flattened, with a small but evident internal laminar expansion; tarsal claws curved, without basal tooth, internal claw slightly longer than external one, protarsomeres 2–5 with tufts of golden setae in the external margin (Fig. 12).

Abdomen: Vestiture leaving a wide and long glabrous oval area at mid-line in ventrites 3–4; and a broader sub-rectangular one in ventrite 5. Ventrites 3 and 4 raised and flattened above, with apex rounded and slightly projected on the next ventrites (Figs 4, 13).

Genitalia: Total length 6.0 mm; phallobase long (length: 2.9 mm width 2.1 mm) narrow with apex of manubrium rounded; parameres long (length: 4.1 mm), broadened at basal 3/5, elongated-oval at apical 2/5, with a deep oval concavity not reaching the apex, with minute teeth in the internal margin at the apical half, getting more abundant apically. Median lobe slightly shorter than the parameres (3.7 mm), broad sub-triangular with rounded apex, with a median sulcus, apex rounded (Fig. 14 a, b).

Sexual dimorphism. Females similar to males but with palpi more slender, anterior tibiae with spurs elongate sub-triangular, tarsal claw long, curved and acute, with a basal acute tooth.

Variation. Body length 32–36 mm, humeral width 17.0–17.5, 18–2.0× longer than wide; coloration can be brown-reddish (in old specimens); sixth antennomere and antennal club can be reddish-yellow to dark red; average length of maxillary palpomeres: 0.04, 0.29, 0.26, 0.15 mm; average width third palpomere: 0.085 mm; average length of labial palpi: 1.8 mm; prosternal lobes with apex rounded to acute; internal spur of protibiae with apex truncate, sometimes without notch in the external margin.

Distribution. Mexico: Colima, Guerrero, Jalisco, Morelos, Nayarit, Oaxaca, Puebla, Veracruz (Fig. 41).

Taxonomic comments. Since this species differs from *H. (D.) ovatus* in characters of key taxonomic importance like the shape of male maxillary palps, the protarsal structure and the male genitalia we consider that these differences support the description of *H. (D.) pseudovatus* as a new species. However, both species seem to share a large part of its distribution in Mexico (Fig. 41). Furthermore, according to Andrew E.Z. Short (personal com-

munication) some *H. (D.) ovatus* specimens from Veracruz, Mexico are somewhat intermediate in morphology with *H. (D.) pseudovatus* **sp. nov.** In order to fully elucidate the nature of the relation between these two species more sampling in Mexico is needed as well as to study their genetic information.

Hydrophilus (Dibolocelus) nucleoensis* Arce-Pérez & Arriaga-Varela **sp. nov.*

Figs. 5, 6; 15–18, 42

Etymology. This new species is named *H. (D.) nucleoensis* because of its distribution on the Central American Nucleus, a natural area formed by mountain ranges that go from the center-south of the state of Chiapas in Mexico to the north of Nicaragua (see Halffter 1987; Halffter & Morrone 2017).

Type material (31 ♂, 28 ♀). **Holotype male: MEXICO: Chiapas:** Reserva Montes Azules [16°50'00"N 91°30'00"O], 14.vii.1989, F. Arias y R. Barba cols. 1 ♂ (CNIN). **Paratipos** mismos datos que el holotipo 6 ♂, 4 ♀ (CNIN); Ocosingo, Corozal, [16°49'16"N 90°53'25"O], 100 msnm 23.v.1984, E. Barrera y A. Ibarra cols. 5 ♂, 4 ♀ (CNIN), Ocosingo, Boca Lacantún, 29.v.1984 [16°34' 50" N, -90° 42' 50"O] 200 msnm, E. Barrera y A. Ibarra cols. 2 ♂, 2 ♀ (CNIN); 24.v.1984, E. Barrera, A. Ibarra y M. García cols. 1 ♂, 1 ♀ (CNIN); 24.v.1984, A. Ibarra col. 1 ♂, 2 ♀ (CNIN); Villa Flores, Villa Flores, [16°14'00"N 93°16'09"O], 500 msnm, 26.iv.1983, R. Fernández col. 1 ♂, 4.x.1983, E. Ríos col. 1 ♂, 19.x.1983, J. Melchor 1 ♀, 8.xi.1983, S. Serrano col. 1 ♀, 13.xi.1983, C.A. col. 1 ♀, 3.vii.1990, G. Morales col. 1 ♂, 20.x.1999, Benjamin C. col. 1 ♀, Copainala, Copainala, 17° 06' norte, 93° 17' Oeste, 440 msnm, 16.v.1997, Arroyo, C.I. Sánchez col. 1 ♀ (IEXA); Palenque, 19.v.1984, [17°30'33"N 91°58'56"O], 60 msnm, A. Ibarra y M. García cols. 1 ♀ (CNIN); Palenque Malla Bell, 20.iv.1988, J. Kemner col. 1 ♀ (IEXA), Acacoyagua, Acacoyagua, [15°21'00"N 92°41'00"O], 277 msnm, i.1999, N. Jimenez col. 1 ♀ (IEXA), Mapastepec, Mapastepec, Rva. La Encrucijada, Laguna Chantutu, 28.viii.2000, 50 msnm, 15° 25' 59" Norte, 92° 53' 52" Oeste C.R. Chamé col. 1 ♀ (IEXA). **Campeche:** Calakmul-Xpuhil [18°30'20"N 89°23'50"O], 29.v.2004, L. Cervantes y C. Mayorga cols. 1 ♂, 1 ♀ (IEXA), Calakmul-Xpuhil, 200 msnm, 15/17.xi.2001, E. Barrera y H. Brailovsky cols. 1 ♀ (CNIN); Calakmul, 24.vii.2014, Selva Alta Perenifolia, Fernando Escobar col. 1 ♂ (IEXA); **Guerrero:** Hwy 200, 5 mi. S. Tecpan, 17°11.2'N, 100 36.7'W, 30 m, 20.vi.2010, D.Brzoska 1 ♂ (SEMC). **GUATEMALA. Escuintla:** San José, [13°55'32"N 90°49'28"O], 4.i.1984, R. Pérez col. 2 ♂; Escuintla, Río San José, 9.vi.1985, E. Pérez col. 1 ♂ (UVGC); **Petén,** San José, October 1991, leg. Frisch, 1 ♂ (SEMC). **NICARAGUA: Río San Juan:** Los Guatusos, río Pepaturro, [10°48'02"N 84°12'39"O], 21/29.v.2000, B. Hernandez y J. Sunyer cols. 2 ♂; Río San Juan, Sarapiquí, 1/5.ix.2006, A. Borges y P. Andino cols. 1 ♀; San Juan, San Carlos, 20.ii.1995, F. Collantes col. 1 ♀ (IEXA). **COSTA RICA: Guanacaste** Prov., Nandayure, nr. Carmona, 10°03'32.9"N, 85°14'58.9"W, 30 m, 15.i.2003, pond, leg. Short, Roughley, & Porras 1 ♂, 1 ♀ (SEMC, INBio); Guanacaste Prov, Rd to Palo Verde, roadside ditch, 11.i.2004, leg. Short & Lebbin, AS-04-027, 1 ♂ (SEMC); **Limon Prov.,** Sector Cedrales de la Rita, 3 km N. Del Puente Rio Suerte, Ruta Puerto Lindo, November 1995, leg. E. Rojas, INBIO-CRI002-378269, 1 ♂ (INBio).

Diagnosis. This species can be distinguished by the following combination of characters: Maxillary palpi clearly long and slender; fifth protarsomere as long as the basal ones together, flattened, with evident internal laminar expansion. This species is very similar to *H. (D.) ovatus* and *H. (D.) pseudovatus* **sp. nov.** but can be distinguished from them by [the characters the characters of *H. (D.) ovatus* and *H. (D.) pseudovatus* are provided in brackets for comparative purposes] the maxillary palpi clearly longer and slender, width of the third palpomere 0.065 (Fig. 15) [*H. (D.) ovatus* and *H. (D.) pseudovatus* **sp. nov.** present maxillary palpi with the third palpomere flattened and widened, with width greater than 0.080 mm (Figs. 7,11)], fifth protarsomere flat and with evident internal laminar expansion (Fig. 16) [without or with slight internal laminar expansion (Figs. 8, 12)], abdominal ventrites 3 and 4 with slender glabrous area at midline (Fig. 17) [ventrites 3 and 4 with wide glabrous area at mid-line (Figs. 9, 13)], abdominal ventrites 3 and 4 raised and slightly acute above at midline (Fig. 17) [abdominal ventrites 3 and 4 raised and flat above at midline (Figs. 9, 13)]; *H. (D.) ovatus* and *H. (D.) pseudovatus* are mainly distributed in the Nearctic portion of Mexico while *H. (D.) nucleoensis* **sp. nov.** is mainly distributed in the Neotropical part of Mexico, extending towards Central America in Guatemala and Nicaragua (Fig. 42).

Description male holotype. Body elongated-fusiform, length 32–37 mm (male holotype: 36 mm), width 17.0–17.5 mm at humeri (holotype: 17.0 mm), 2.1× longer than wide, dorsally strongly convex and glabrous, ventrally flat and pubescent; dorsal color black with dark green hue; ventrally black with reddish hue, ventral vestiture pale yellow; antennae, palpi and legs black with reddish hue (Figs 5, 6).

Head: Antennae short with nine antennomeres, scape large and robust, longer than the next four antennomeres together, pedicel subequal to the following three antennomeres, sixth antennomere long and oval, subequal to the previous four together, not covering the first article of antennal club (Fig. 15). Maxillary palpi long and slender, with four palpomeres, with lengths: 4.0, 3.1, 2.8, 1.6 mm; first palpomere small, sub-conical, second long, curved, slightly broadened towards apex, third shorter and wider, slightly flattened towards apex, with 0.060 mm in its wider side, fourth short, oval, with truncated apex. Mentum hexagonal, 1.7× wider at base than long, lateral margins parallel at basal half, apically converging straightly, apex truncated and straight. Labial palpi short, length of palpomeres: 0.02, 0.09, 0.06 mm; first palpomere very small and subconical, second long and slightly broadened towards apex, 1.2× longer than the third, with short golden setae near the internal margin, third palpomere short and oval, with apex rounded (Fig. 15).

Thorax: Prosternal lobes raised and apically rounded, with short reddish-yellow setae at apex; mesoventrite with broad keel, with lateral margins rounded and convergent towards apex, with a broad and shallow concavity at basal half, deeper towards apex. Metaventrite with keel wide and flat, with feeble median longitudinal groove, ending as a long spine reaching half-length of the second abdominal ventrite (Fig. 6). Each elytron with two well-marked rows of black spots, one sublateral starting after the humerus, and other more incomplete on the sides (Fig. 5).

Legs: Anterior tibiae with two spurs; internal one shortest, flat, sub-rectangular with apex truncate straight; external spur longer, sub-triangular, acute; fifth protarsomere as long as the basal ones together, flattened, with evident internal laminar expansion; tarsal claws curved, without basal tooth, internal claw slightly longer than external one, protarsomeres 2–5 with tufts of golden setae in the external margin (Fig. 16).

Abdomen: Vestiture leaving a long oval glabrous area at mid-line in ventrites 3–4; and a broader sub-rectangular one in ventrite 5. Ventrites 3 and 4 raised and slightly acute above, with apex slightly rounded and projected on the next ventrites. (Figs 6, 17); ventrite 5 raised and slightly sharp above.

Genitalia: Total length 6.05 mm; phallobase long (length: 2.85 mm, width 2.25 mm) narrow with apex of manubrium rounded; parameres long (length: 4.25 mm), distinctly broadened at basal 3/5, elongated-oval at apical 2/5, with a deep oval concavity not reaching the apex, with minute teeth in the internal margin at the apical half, getting more abundant apically. Median lobe slightly shorter than the parameres (3.75 mm), broad sub-triangular, with a median sulcus, apex rounded (Fig. 18 a, b).

Sexual dimorphism. Females similar to males but with narrow maxillary palpi, anterior tibiae with long sub-triangular spurs, tarsal claws curved and acute, with and basal acute tooth.

Variation. Body length between 32–37 mm, width 17.0–17.5 mm, 1.8–2.0× longer than wide; body color can be dark brown with yellow-reddish hue (in old specimens); average length of maxillary palpomeres: 4.0, 3.0, 2.9 and 1.6 mm; average width of third maxillary palpomere: 0.65 mm; total length of labial palp: 1.8 mm.

Distribution. Mexico: Campeche, Chiapas, Guatemala: Escuintla and Nicaragua: Río San Juan (Fig. 42).

***Hydrophilus (Dibolocelus) violaceonitens* Jacquelin du Val, 1857 status restored**

Figs. 19, 20; 25–28, 37–40, 43, 46–49.

Hydrophilus violaceo-nitens Jacquelin du Val, 1857: 49.

Stethoxus (Dibolocelus) violaceonitens (Jacquelin du Val); Bedel, 1891: 314.

Hydrous (Dibolocelus) violaceonitens (Jacquelin du Val); Kuwert, 1893: 83.

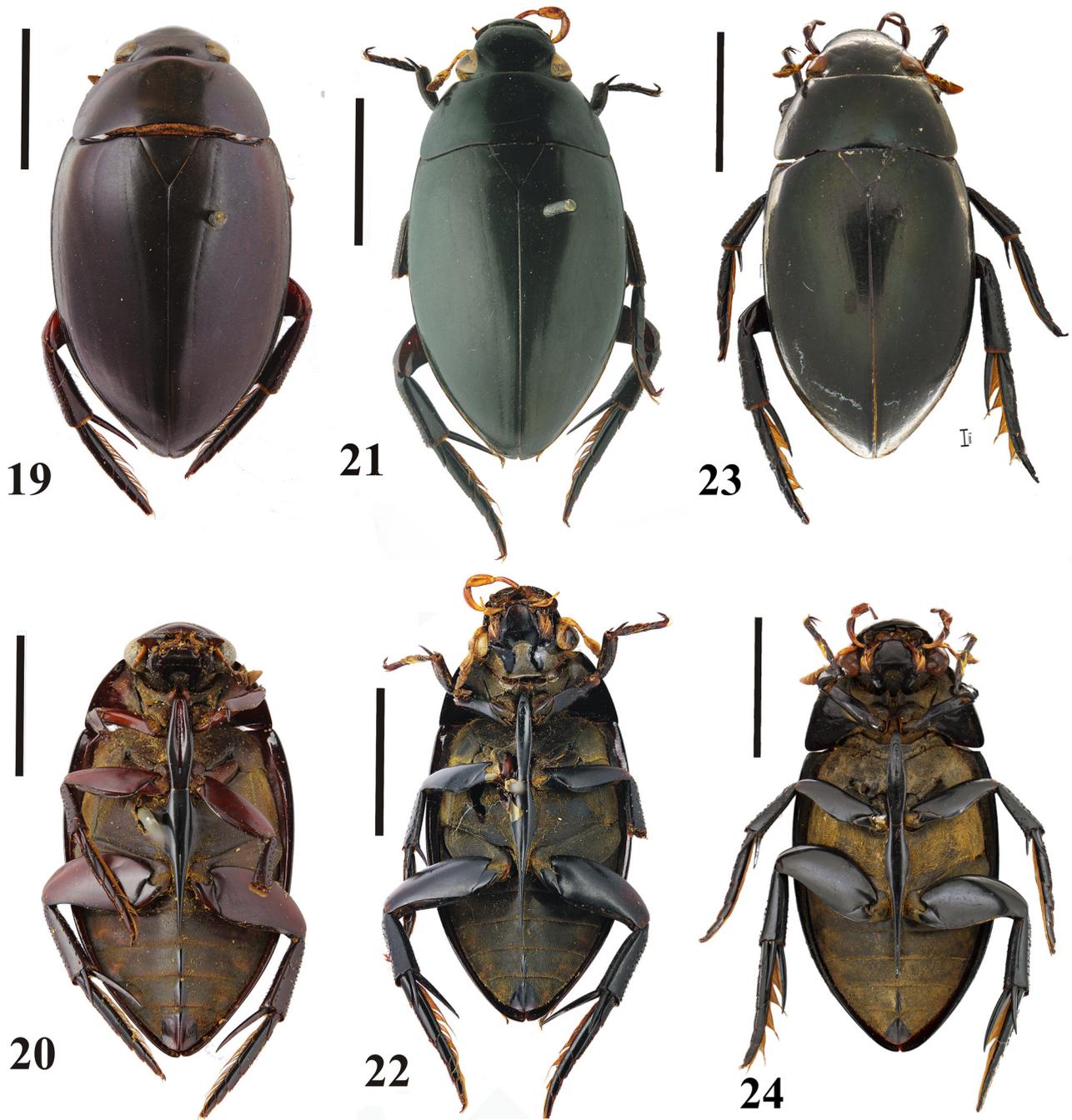
Hydrophilus (Dibolocelus) smaragdinus Brullé. Syn.: Régimbart, 1901: 227.

Hydrophilus (Dibolocelus) smaragdinus Brullé (in part), Hansen, 1999: 162.

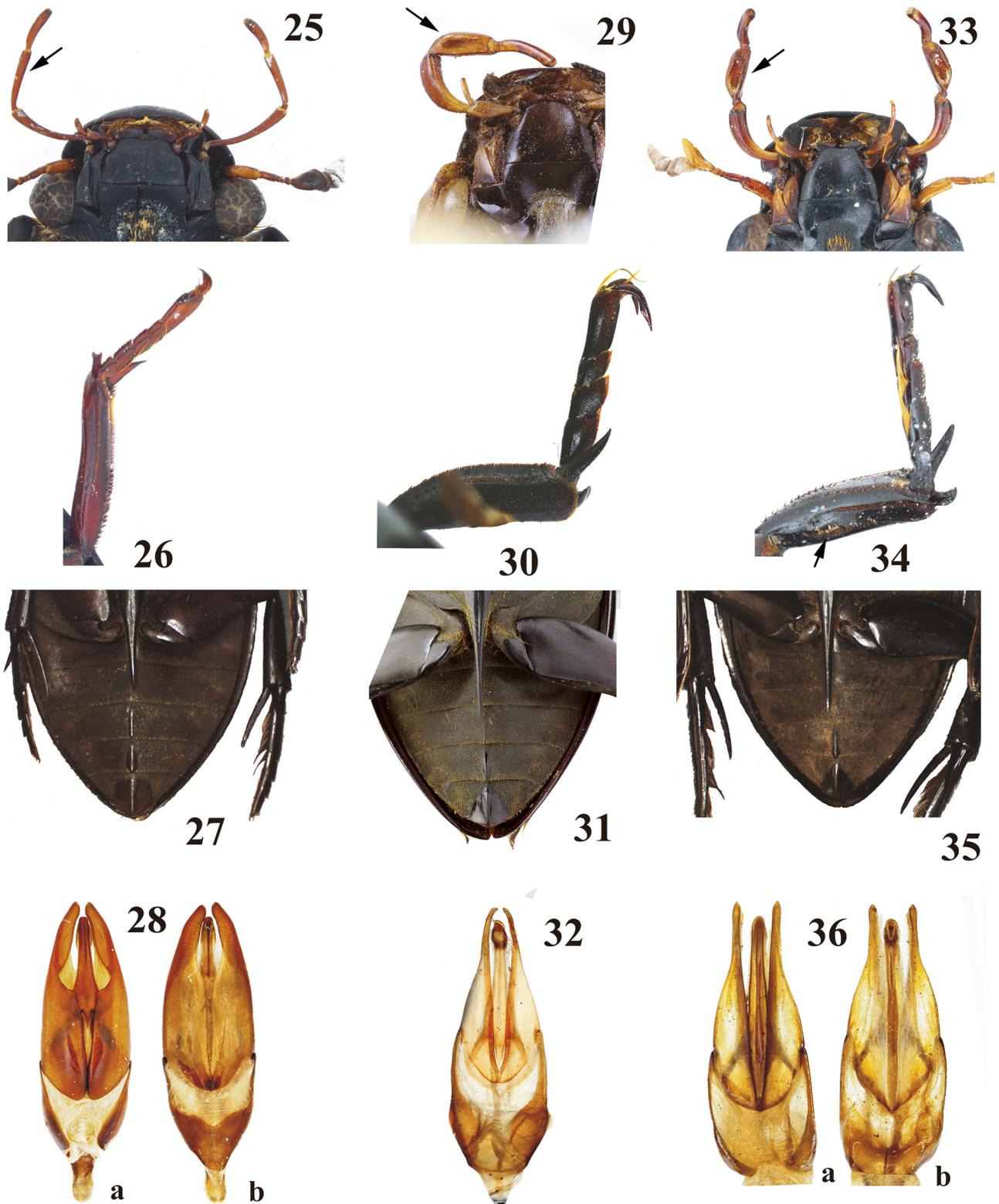
Type material. [Studied through photographs] Female? holotype, MNHN: “Cuba / C. Chevrolat”, “Type”, “*Hydrophilus / violaceo-nitens*”, “*smaragdinus* Br. / v. *violaceo nitens* Duv.”, “MUSÉUM PARIS / 1922 / coll. L. Bedel”, “HOLOTYPE/ *Hydrophilus / violaceonitens* Jacquelin du / Val, 1857” / “MNHN, Paris/ EC11750/ [barcode]”. [Specimen is damaged; maxillary palpi, mesotarsi and left metatarsus are missing]

Additional material (19♂, 6♀). MEXICO: Campeche: Kalkiní, El Remate, [20°22'21"N, 90°03'03"O] 26.iv.1982, M. García col. 3♂, 2♀ (CNIN); El Remate, entre raíces de manglar, 12.xii. 2020, S. Ospina col. 1♂ (IEXA); Chiapas: Salto de Agua [17°33'00"N 92°20'00"O] iv.1907, C.C. Hoffmann col. 1♂ (CNIN); Quintana Roo: Tulum [20°12'43"N 87°27'57"O], .xi. 1981, E. Pech col. 2♂ (CNIN); Puerto Morelos, [20°51'13"N 86°52'31"O] Gasolinera, 10.vii.1983, O. Canul col. 2♂ 1♀ (CNIN); El Naranjo, Selva alta, 7.vii.1985, A. Cadena y Conde

cols. Noct. 1♀ (IEXA); F. Carrillo Puerto, [19°34'43"N 88°02'43"O] Laguna Chunyaxche, 30.viii.1988, Fernández y Barba cols. 1♂ (CNIN); F. Carrillo Puerto, 2.x.1983, 1♂ (IEXA); Puerto Morelos, [20°51'13"N 86°52'31"O 1.v.1982] V. Meléndez col. 1♂, 1♀(CNIN); **Tabasco:** Villa Hermosa, Macultepec [18°09'00"N 92°52'00"O], v.1953, J. Hendrichs col.1♂ (CNIN); **Veracruz:** Las Choapas, [17°54'00"N 94°05'24"O], 28.v.1976, E. Barrera col. 1♂,1♀(CNIN); Las Choapas, 28.i.1980, Sánchez Aguilera col. 1♂ (IEXA); Tecolutla, Flores Magón, [20°23'17"N 97°01'31"O], 13.x.2001, Cabrera col. 1♂ (IEXA); Actopan, La Mancha [19°30'13"N 96°37'09"O], 24.v.2002, a la luz, R. Arce col. 1♂ (IEXA); Mexico, Vera Cruz, Flohr / B.C.A. Col. I. 2. *Hydrophilus violaceo-nitens*, Jaquelin du Val 2♂ (BMNH). **CUBA:** **Provincia Matanzas**, Playa Girón, Martin Vyklicky leg. 19.v.2004 1♂ (NMPC).



FIGURES 19–24. Dorsal and ventral view of *Hydrophilus (Dibolocelus)* spp. 19–20 *H. (D.) violaceonitens* status restored; 21–22 *H. (D.) pollens* Sharp; 23–24 *H. (D.) cf. purpurascens* (Régimbart).



FIGURES 25–36. Morphological structures and male genitalia of *Hydrophilus (Dibolocelus)* spp. **25–28** *H. (D.) violaceonitens* sp. nov.; **25** ventral view of head (arrow: third labial palpomere); **26** protibia and tarsi, **27** ventral view of abdomen; **28a** aedeagus ventral; **28b** aedeagus dorsal; **29–32** *H. (D.) pollens* Sharp; **29** ventral view of head (arrow: third labial palpomere); **30** protibia and tarsi, **31** ventral view of abdomen; **32** aedeagus ventral; **33–36** *H. (D.) cf. purpurascens* (Régimbart); **33** ventral view of head (arrow: third labial palpomere); **34** protibia and tarsi (arrow: subrectangular row of hard setae); **35** ventral view of abdomen; **36a** aedeagus ventral; **36b** aedeagus dorsal.



FIGURES 37–40. Comparison of morphology between *H. (D.) violaceonitens* and *H. (D.) smaragdinus* Brullé (from Brazil); **37–38** *H. (D.) violaceonitens* **status restored**; **37** ventro-lateral view of pro- and mesothorax (arrow: apically truncate prosternal lobes); **38** ventral view abdomen and hind tibia (arrow: tibial apex without patch of setae); **39–40** *H. (D.) smaragdinus* Brullé (from Brazil); **39** ventro-lateral view of pro- and mesothorax (arrow: acute apex of prosternal lobes); **40** ventral view abdomen and hind tibia (arrow: patch of setae in tibial apex).

Diagnosis. This species can be distinguished by the following combination of characters: Maxillary palpi long and narrow; anterior tibiae with internal spur sub-rectangular with bifid apex; fifth protarsomere shorter than basal ones together, without internal projection or expansion. This species can be distinguished from *H. (D.) smaragdinus*

Brullé a species from South America with which it was synonymized until now, by [characters of *H. (D.) smaragdinus* provided in brackets for comparative purposes]: *H. (D.) violaceonitens* without setose patch in the apical region of hind tibiae of males (Fig. 38) [*H. (D.) smaragdinus* has a dense patch of short setae in the medial apical region of the posterior tibiae in males (Fig. 40)]; prosternal lobe sharply truncated apically (Fig. 37) [prosternal lobes apically acute (Fig. 39)]; ventrites 3–5 raised but not forming a sharp keel (Figs. 20, 27), [ventrites 3–5 raised as a sharp keel]; fifth protarsomere with straight internal margin and with reduced number of suction cups (Fig. 26) [fifth protarsomere wide with rounded internal margin, and with numerous suction cups]; male genitalia wide, parameres broad, abruptly narrowed towards apex, with a long internal oval concavity in the apical third, and with subapical elongated-oval gonopore (Fig. 28 a, b) [male genitalia slender with narrow parameres gradually tapering towards apex, and apex slightly widened]. Additionally, among the Mexican species *H. (D.) violaceonitens* is externally more similar to *H. (D.) nucleoensis* **sp. nov.**, but differs from it by [the characters of *H. (D.) nucleoensis* provided in square brackets for comparative purposes]: in *H. (D.) violaceonitens* the mentum is broad, with parallel lateral margins in the basal half and in the apical half markedly curved, the apical margin truncated and slightly concave (Fig. 25) [mentum not wide, with lateral margins parallel and slightly curved in the basal half, apically markedly convergent, the apical margin truncated and straight (Fig. 15)]; fifth protarsomere shorter than the previous ones together and without internal projection (Fig. 26) [fifth protarsomere as long as the previous ones together, flat and with an evident internal laminar expansion (Fig. 16)]; anterior tibiae with sub-rectangular internal spur with bifid apex (Fig. 26) [anterior tibiae with sub-rectangular internal spur with straight and truncated apex (Fig. 16)].

Redescription. Body elongated-fusiform, length 33 mm, width 17 mm at humeri, 1.9× longer than wide, dorsally strongly convex and glabrous, ventrally flat and pubescent; dorsal color black with dark green hue; ventrally black with reddish hue, ventral vestiture reddish yellow; antennae and palpi reddish yellow, legs black with reddish hue (Figs 19, 20).

Head: Antennae short with scape large and robust, longer than the next four antennomeres together, pedicel subequal to the following three antennomeres together, sixth antennomere long and oval, subequal to the previous four together, not covering the first article of antennal club. Maxillary palpi long and slender, with four palpomeres with lengths: 3.0, 2.8, 2.0, 1.5 mm; first palpomere small, sub-conical, second long, curved, slightly broadened towards apex, third similar to the previous one but shorter, fourth short, oval, with truncated apex. Mentum hexagonal, 2× wider at base than long, lateral margins parallel at basal half, apically markedly curved, apex truncated and slightly concave. Labial palpi short, length of palpomeres: 0.2, 0.8, 0.6 mm; first palpomere very small and subconical, second long and slightly broadened towards apex, 1.3× longer than the third, with short golden setae near the internal apex, third palpomere short and oval, with apex rounded (Fig. 25).

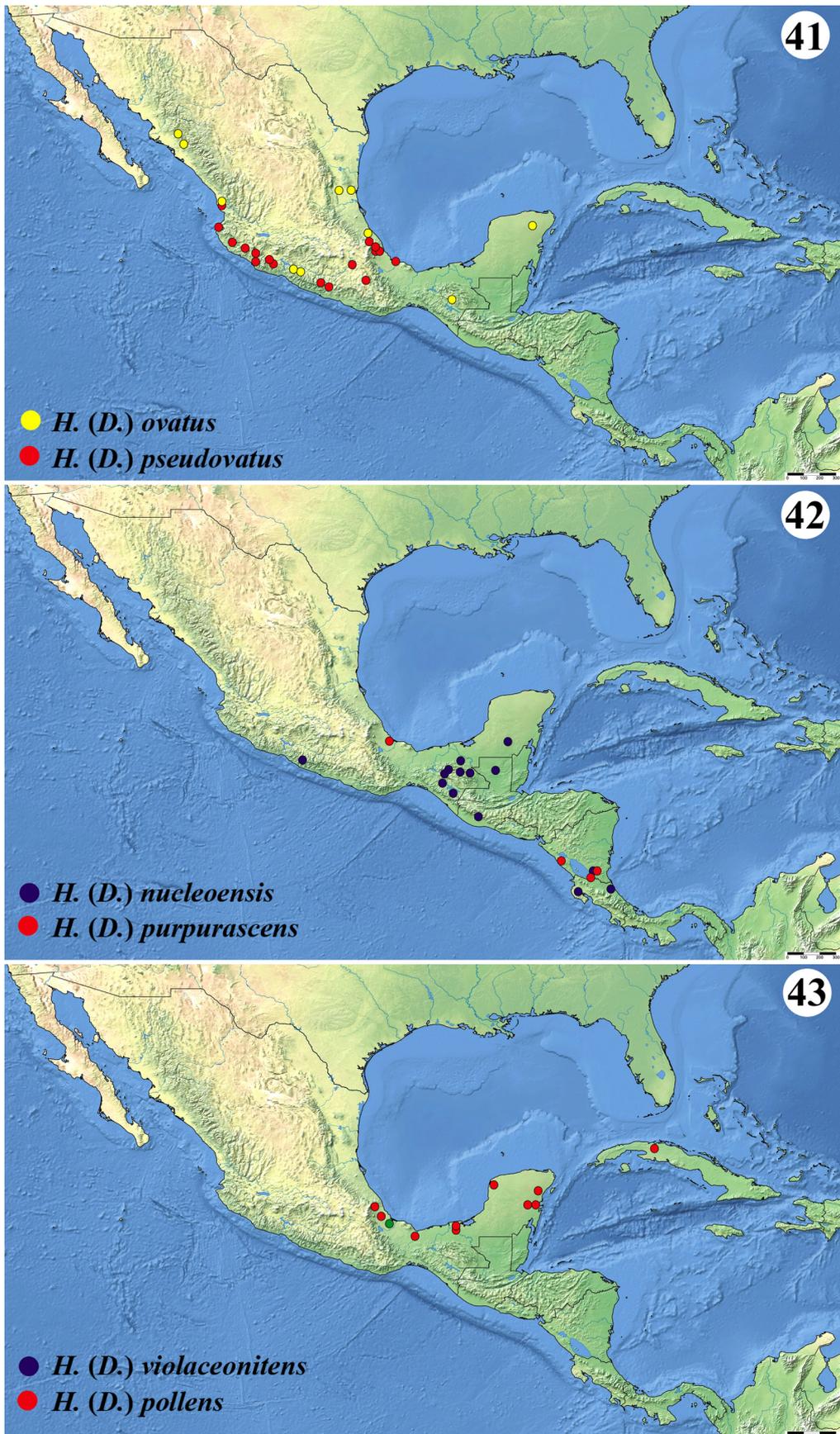
Thorax: Prosternal lobes raised and apically obtusely truncate, with long reddish-yellow setae at anterior margin of apex (Fig. 37); mesoventrite with broad keel, with lateral margins rounded and convergent towards apex, with a deep oval concavity at basal half, deeper towards apex (Fig. 37) and with transverse striae. Metaventrite with keel wide and flat, with feeble median longitudinal groove, ending as a short spine reaching 3/4 of the second abdominal ventrite (Fig. 20). Each elytron with two well-marked rows of black spots, one sublateral starting after the humerus, and other incomplete on the sides (Fig. 19).

Legs: Anterior tibiae with internal spur shortest, flat, sub-rectangular with apex bifid, external spur longer, sub-triangular, acute; fifth protarsomere shorter than basal ones together, without projections, tarsal claws curved, without basal tooth, internal claw slightly longer than external one, all protarsomeres with tufts of golden setae in the external margin, fifth protarsomere bearing a small apical ventral spine (Fig. 26), hind tibia without setose patch (Fig. 38).

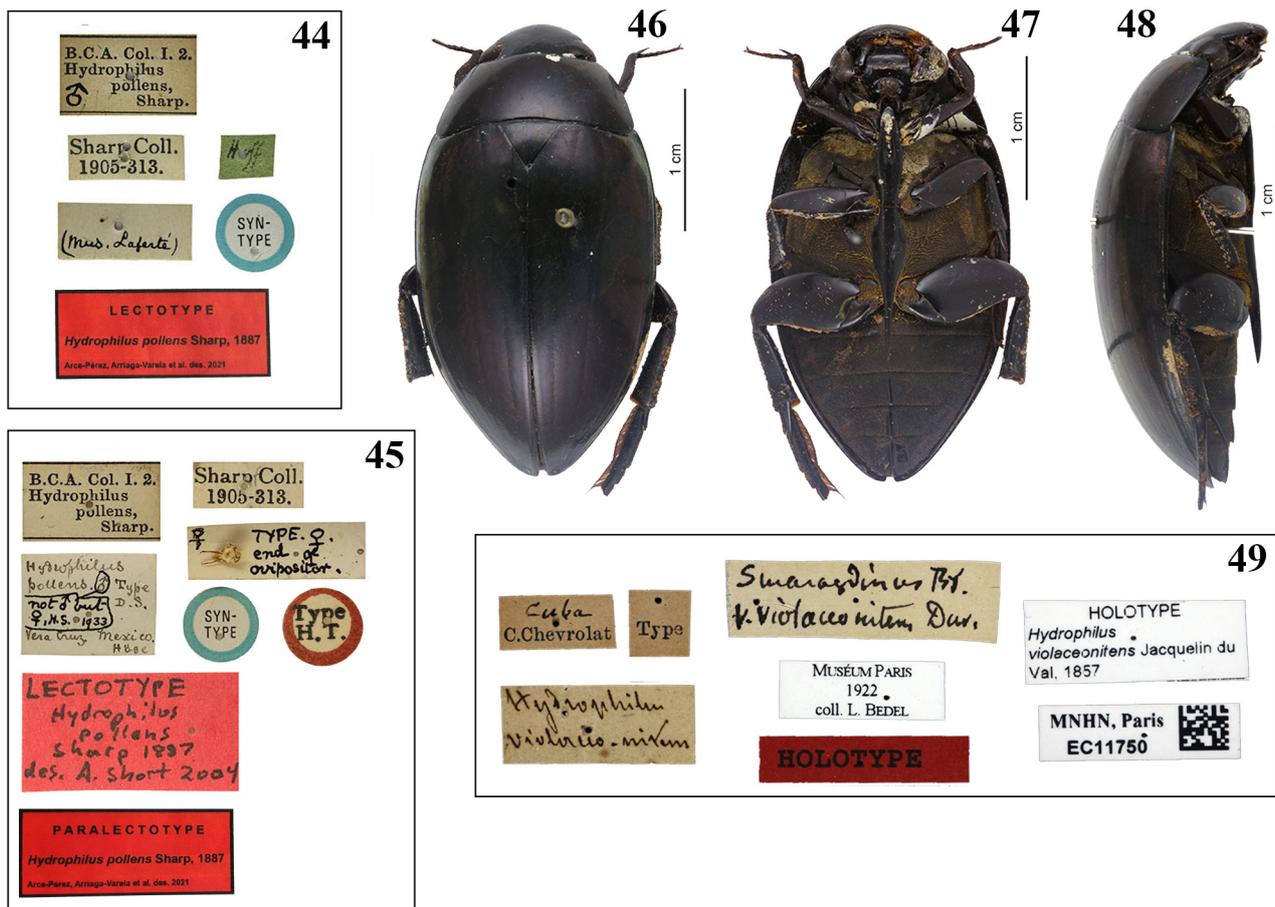
Abdomen: Vestiture leaving a slender and long glabrous oval area at mid-line in ventrites 3–4; and a broader sub-rectangular one in ventrite 5. Ventrites 3 and 4 raised and slightly acute above, with its apex slightly acute and projecting over the next ventrite, ventrite 5 raised and subacute medially (Fig. 27).

Genitalia: Total length 5.2 mm; phallobase long (length: 2.25, width 1.85 mm), narrow, with apex of manubrium rounded; parameres long (length: 4 mm), broadened at basal 3/5, elongated-oval at apical 2/5, with a deep oval concavity not reaching the apex, with minute teeth in the internal margin at the apical half, getting more abundant apically; median lobe slightly shorter than the parameres (3.7 mm), broad sub-triangular, with a median sulci, apex rounded (Fig. 28a,b).

Sexual dimorphism. Females similar to males but with narrow maxillary palpi, anterior tibiae with long sub-triangular spurs, tarsal claws curved and acute, with and basal acute tooth.



FIGURES 41–43 Geographical distribution of *Hydrophilus (Dibolocelus)* spp. in Mexico and Central America; **41** red circles: *H. (D.) pseudovatus* **sp. nov.**, yellow circles: *H. (D.) ovatus* Gemminger & Harold; **42** blue circles: *H. (D.) nucleoensis* **sp. nov.**, red circles: *H. (D.) cf. purpurascens* (Régimbart); **43** red circles: *H. (D.) violaceonitens*, green circle: *H. (D.) pollens* Sharp.



FIGURES 44–49. Type material and labels of *Hydrophilus (Dibolocelus)* from Mexico. 44 Specimen labels of *Hydrophilus (Dibolocelus) pollens* Sharp male lectotype (designated in this work); 45 Labels of female paralectotype; 46–48 Habitus of *Hydrophilus (Dibolocelus) violaceonitens* du Val; 46 dorsal; 47 ventral; 48 lateral; 49 Specimen labels of *Hydrophilus (Dibolocelus) violaceonitens* du Val holotype. Copyright of images 46–49 belongs to MNHN/Christophe Rivier.

Variation. Body length between 27–33 mm, width 16.5–17.5 mm, 1.8–1.9× longer than wide; dorsal body color from dark greenish to black, ventral color can be dark reddish to black, sixth antennomere and antennal club from reddish yellow to pitch black; average length of maxillary palpomeres: 3.0, 2.7, 2.0 and 1.4 mm; total length of labial palpi: 1.8 mm.

Taxonomic comments. This species was originally described by Jacquelin du Val (1845) from Cuba, and later recorded in Mexico by Sharp (1887) based on two specimens from Veracruz. Later Régimbart (1901) synonymized it under *H. (D.) smaragdinus* Brullé a species described from South America. Currently *H. (D.) smaragdinus* is recorded from several countries in the Neotropical Region: Bolivia, Brazil, French Guiana, Peru, Venezuela, Cuba and Mexico (Bachmann 1968; Hansen 1999). Although, unfortunately we did not have the chance of directly studying the holotype deposited in Museum National d’histoire Naturelle, Paris, we had access to high-definition photographs of the probably female holotype kindly provided by the curators of the museum (Figs 46–49). After its study and the thorough examination of the morphology of the specimens from Veracruz studied by Sharp, multiple other specimens from Mexico, one recently collected specimen from Cuba, and its comparison with specimens of *H. (D.) smaragdinus* from Brazil and Venezuela (AOBC, NMPC), identified by A.O. Bachmann and Martin Fikáček respectively (Figs 37–40), we conclude that the specimens from Cuba and Mexico are not conspecific with *H. (D.) smaragdinus* Brullé, therefore the restoration of *H. (D.) violaceonitens* as a valid species is fully justified. The present description of this species is based on a male from Mexico (Veracruz, La Choapas) compared to the material that Sharp (1887) cited from Veracruz and to a male specimens from Cuba (Matanzas, 1♂) and other specimens from Mexico.

Distribution. Cuba: Matanzas; Mexico: Campeche, Chiapas, Quintana Roo, Tabasco, Veracruz (Fig. 43)

Hydrophilus (Dibolocelus) pollens Sharp, 1887

Figs. 21, 22; 29–32, 43.

Hydrophilus pollens Sharp, 1887: 762.

Dibolocelus pollens (Sharp); Régimbart, 1901b: 665.

Hydrous (Dibolocelus) pollens (Sharp); Zaitzev, 1908: 367.

Type material (1♂, 1♀): male lectotype, BMNH: B.C.A. Col. I. 2. *Hydrophilus pollens*, Sharp. / Sharp Coll. 1905-313 / hoff / Mus. Laferté / Syntype / LECTOTYPE, *Hydrophilus pollens* Sharp, Arce-Pérez, Arriaga-Varela et al. Des. 2021; female paralectotype, BMNH: *Hydrophillus pollens* ♂ [not ♂ but ♀, H.S. 1933], Vera Cruz, Mexico. Höge / B.C.A. Col. I. 2. *Hydrophilus pollens*, Sharp. / [ovipositor in slide] ♀, TYPE ♀, end of ovipositor / Syntype / Type H.T. / LECTOTYPE *Hydrophilus pollens* Sharp 1887, des. A. Short, 2004 / PARALECTOTYPE, *Hydrophilus pollens* Sharp, Arce-Pérez, Arriaga-Varela et al. Des. 2021.

Diagnosis. This species can be distinguished by the following combination of characters: maxillary palpi robust, inflated, with third palpomere with a deep ventral excavation; anterior margin of mentum rounded. Fifth protarsomere shorter than basal ones together, without laminar expansion. Protarsal claws moderately long, curved, expanded at distal 2/5, apex markedly acute. This species is very similar to *H. (D.) cf. purpurascens*, but can be distinguished by [the characters of *H. (D.) cf. purpurascens* are provided in square brackets for comparative purposes] *H. (D.) pollens* being dorsally black with greenish hue (Fig. 21) [dark green with purple reflections (Fig. 23)]; anterior margin of mentum rounded (Fig. 29) [truncated and straight (Fig. 33)]; protarsal claws expanded to 2/5 apical and apically acute (Fig. 30) [claws not expanded, only acute (Fig. 34)]; the metaventral spine shorter, not exceeding 1/2 of the third abdominal ventrite (Fig. 22) [metaventral spine longer, reaches or exceeds the posterior margin of the third abdominal ventrite (Figs. 24)]; ventrites 3 to 5 with a sharp and glabrous crest (Fig. 31) [ventrites 4 and 5 with a thick and glabrous crest (Fig. 35)]; slender parameres, slightly directed inward and with their apex truncated and directed inward (Fig. 32) [parameres thick, slightly directed outward and with apex broad sub-triangular (Fig. 36)].

Redescription. Body elongated-fusiform, length 34–39 mm, width 15–16 mm at humeri, 2.2–2.3× longer than wide, dorsally strongly convex and glabrous, ventrally flat and pubescent; dorsal color black with dark green tone, more evident under direct light; ventrally black with reddish hue, ventral vestiture pale yellow; antennae, yellow, palpi dark yellowish-red, legs black with slight purplish hue, femora with dorsal surface and apices of ventral surface reddish (Figs. 21, 22).

Head: Antennae short with scape large and robust, slightly flattened, longer than the next four antennomeres together, pedicel subequal to the following three antennomeres together, sixth antennomere long and oval, subequal to the previous four together, almost completely covering the first article of antennal club. Maxillary palpi long and robust, with four palpomeres with lengths: (0.5, 2.5, 2.1, 1.9 mm); first palpomere small and globose, second robust, markedly curved and broadened towards apex, third globose, about 2.1× longer than wide, wider at basal third, with a deep and broad ventral excavation from base to apex, fourth short, slender, subcylindrical, slightly curved and with truncated apex. Mentum hexagonal elongate, 1.5× wider at base than long, lateral margins parallel, anterior margin rounded. Labial palpi short, length of palpomeres: 0.2, 1.8, 1.1 mm; first palpomere very small and broad, second long, inflated, sub-triangular and widening apically, 1.6× longer than the third, with a tuft of long golden setae near the outer margin, third palpomere shorter, comparatively narrow with truncate apex (Fig. 29). **Thorax:** Prosternal lobes raised with apex with acute tooth directed ventrally, with short reddish-yellow setae near apex; mesoventrite with broad keel, with lateral margins slightly rounded and rather parallel towards apex, with a long and shallow oval concavity in the basal 3/5, deeper towards the apex. Metaventricle with keel wide and slightly convex, with feeble median longitudinal groove, ending as a long spine reaching half-length of the third abdominal ventrite (Fig. 22). Each elytron with two well-marked rows of black spots, one sublateral starting after the humerus, and other more incomplete on the sides (Fig. 21).

Legs: Anterior tibiae with internal one spur shortest, flat, sub-rectangular with truncate and straight apex, external spur longer, sub-triangular, acute; fifth protarsomere shorter than basal ones together, slightly flattened, without projections; tarsal claws long curved, expanded into apical 2/5, then markedly acute, without basal tooth, internal claw slightly longer than external one; protarsomeres 2, 3 and apex of 5 with tufts of golden setae in the external margin (Fig. 30).

Abdomen: Vestiture leaving a slender and long oval glabrous area at mid-line in ventrites 3–4; fainter in ventrite 3, and broader sub-triangular one in ventrite 5. Ventrite 3 raised and with a small glabrous line in posterior half, ven-

trite 4 with an acute keel in the posterior 3/4 projecting over next ventrite as a short spine; ventrite 5 with an acute keel along all its length at mid-line (Fig. 31).

Genitalia: Total length 4.8mm (holotype); phallobase long (length: 2.3 width 1.2 mm) narrow with apex of manubrium rounded; parameres long (length: 4.2 mm), broadened at basal 3/5, and markedly narrowed at apical 2/5, directed internally, with apex truncate and; median lobe elongate sub-triangular, slightly shorter than the parameres, with an elongate sclerite at mid-line (Fig. 32a, b).

Sexual dimorphism. Females similar to males but with narrow maxillary palpi, third labial palpomere not inflated nor excavated. Protibiae with internal spine not truncate, acute, slightly shorter than external. Tarsal claws curved and acute with an acute basal tooth.

Distribution. Mexico: Veracruz (Fig. 43), Guyana.

Taxonomical comments. This species was described by Sharp (1887: 762), based on a very small number of specimens and diagnostic characters. Unfortunately, there are no recent specimens known, and our redescription is based only on the type material of *H. (D.) pollens* Sharp, deposited in the Natural History Museum of London (BMNH). This species and *H. (D.)* cf. *purpurascens* appear to be the only species in Mexico and Central America belonging to the group of species with the third maxillary palpomere inflated and a strong ventral concavity (Figs. 29, 33). A female syntype has been previously labelled as the holotype apparently based on a misidentification of the sex of the specimen (Fig. 45). Nevertheless, in the original description Sharp (1887) did not mention any specimen in particular as being the holotype. Additionally, this female syntype bears a lectotype label by Andrew E.Z. Short (Fig. 45). This lectotype designation was, however, unpublished. Here we designate the male syntype as the lectotype in order to fix the identity of the species (Fig. 44). A specimen from Demerara, Guyana was part of the original series studied by Sharp. Since it is a female its identity cannot be confirmed beyond a doubt as well as its relation to the Mexican specimens. Nevertheless, its identity preliminary remains as originally intended by Sharp. Other species from South America are probably close to *H. (D.) pollens*. On his treatment of Venezuelan *Hydrophilus* Bachmann (1969) illustrated the genitalia of *H. (D.) purpurascens* Régimbart and the figure suggest a very close resemblance to *H. (D.) pollens*. However, Bachmann (1969) did not study the type specimens of any of the species treated therein. Type series of *H. (D.) purpurascens*, held in MNHN, is composed of females or specimens with broken appendages, and its genitalia has not been studied (Andrew E.Z. Short personal communication). Similarly, the study of the types of *H. (D.) palpalis viridis* (Régimbart) (MNHN) suggest a strong external resemblance with *H. (D.) pollens* but its male genitalia have not yet been studied or illustrated (Andrew E.Z. Short personal communication). The nature of the relationship between these species remains to be solved through a detailed study of type specimens of South American species.

***Hydrophilus (Dibolocelus) cf. purpurascens* (Régimbart, 1901)**

Figs. 23, 24; 33–36, 42.

Dibolocelus palpalis var. *purpurascens* Régimbart, 1901: 223.

Hydrous (Dibolocelus) palpalis var. *purpurascens* (Régimbart); Zaitzev, 1908: 367.

Hydrophilus palpalis s. *purpurascens* (Régimbart); Blackwelder, 1944: 171.

Dibolocelus purpurascens Régimbart; Bachmann, 1969: 284.

Studied material (7♂, 4♀): Mexico: Veracruz: Alvarado, La Barranca, Rancho la Fiaca, 14.iv.2001, M. Aragón col. 1 ♂ (IEXA). **Nicaragua: León,** luz UV. 23.i.1993, Pogatshnik col 1 ♂; León, V-1988, Maes col. 1 ♂, 1 ♀; León, III-1990, Garcete col. 1 ♀; León, vi.1989, Maes col. 1 ♀ (IEXA); **Río San Juan:** Los Guatuzos, Río Papaturo, 40 m, UTM 16P 0712685-1220212, 17/24.iii.2000, Maes, Sunyer y Hernández cols. 2 ♂, 1 ♀; Río San Juan, San Carlos 21.ii.1995, F. Collantes col. 2 ♂.

Diagnosis. This species can be distinguished by the following combination of characters: Maxillary palpi robust, inflated, with third palpomere with a deep ventral excavation; anterior margin of mentum truncated and straight; anterior tibiae with a row of hard setae that form a subrectangular plate (comb-like) near the internal base (Fig. 34); fifth protarsomere about as long as basal ones together, slightly flattened, without laminar expansion. This species is very similar to *H. (D.) pollens* but can be distinguished by [the characters of *H. (D.) pollens* are provided in square brackets for comparative purposes] *H. (D.)* cf. *purpurascens* being dorsally dark green with purple reflections (Fig.23) [is dorsally black with greenish hue (Fig. 21)]; anterior margin of mentum truncated and straight (Fig. 33)

[anterior margin of mentum rounded (Fig. 29)]; protarsal claws not expanded, only acute (Fig. 34) [claws expanded to 2/5 apical and apically acute (Fig. 30)]; metaventral spine longer, reaches or exceeds the posterior margin of the third abdominal ventrite (Figs. 24) [the metaventral spine shorter, not exceeding 1/2 of the third abdominal ventrite (Fig. 22)]; ventrites 4 and 5 with a thick and glabrous crest (Fig. 35) [ventrites 3 to 5 with a sharp and glabrous crest (Fig. 31)]; parameres thick, slightly directed outward and with apex broad sub-triangular (Fig. 36) [slender parameres, slightly directed inward and with their apex truncated and directed inward (Fig. 32)].

Description. *Body* elongated-fusiform, length 33–38 mm, width 17–18 mm at humeri, 2.0× longer than wide, dorsally strongly convex and glabrous, ventrally flat and pubescent. Dorsal color black with dark purple tone (purple tone was not observed clearly in old specimens), ventrally black with reddish hue, ventral vestiture pale yellow; antennae, yellow, palpi yellowish-red, legs black with reddish hue (Figs 23, 24).

Head: Antennae short with scape large and robust, slightly flattened, longer than the next four antennomeres together, pedicel subequal to the following three antennomeres together, sixth antennomere long and oval, with external margin subequal to the previous four together, almost completely covering the first article of antennal club. Maxillary palpi long and slender, with four palpomeres with lengths: 0.5, 2.8, 2.3, 2.1 mm; first palpomere small and globose, second robust, markedly curved and broadened towards apex, third globose, about 2.1× longer than wide, wider at basal third, with a deep and broad ventral excavation from base to near apex, fourth short, slender, subcylindrical, slightly curved and with truncated apex. Mentum hexagonal, 1.6× wider at base than long, lateral margins parallel, anterior margin slightly curved inwards, apex truncated and straight. Labial palpi short, length of palpomeres: 0.2, 1.7, 1.2 mm; first palpomere very small and broad, second long, inflated, sub-triangular and widening apically, 1.4× longer than the third, with a tuft of long golden setae near the outer margin, third palpomere shorter, comparatively narrow with truncate apex (Fig. 33).

Thorax: Prosternal lobes raised with apex with acute tooth directed ventrally, with short reddish-yellow setae near apex; mesoventrite with broad keel, with lateral margins slightly convergent towards apex, with an elongate-oval shallow concavity at basal 4/5, deeper towards apex. Metaventrite with keel wide and convex, with rounded lateral margins, ending as a long spine reaching the posterior margin of the third abdominal ventrite (Fig. 24). Each elytron with two well-marked rows of black spots, one sublateral starting after the humerus, and other more incomplete on the sides (Fig. 23).

Legs: Anterior tibiae with a row of hard setae that form a subrectangular plate (like comb) near the internal base; with internal one spur shortest, flat, sub-rectangular with truncate apex, external spur longer, sub-triangular, acute; fifth protarsomere about as long as basal ones together, slightly flattened, without projections; tarsal claws long, curved, without basal tooth, internal claw slightly longer than external one; protarsomeres 2, 3 and apex of 5 with tufts of golden setae in the external margin (Fig. 34).

Abdomen: Vestiture leaving a slender oval glabrous area at mid-line in ventrite 4, and broader sub-triangular one in ventrite 5. Ventrite 4 with a wide keel in the posterior 3/4 projecting over next ventrite as a short spine; ventrite 5 with a slightly acute keel along all its length at mid-line (Fig. 24, 35).

Genitalia: Total length 4.7 mm (holotype); phallobase long (length: 2.75 width 1.6) narrow with apex of manubrium rounded; parameres long (length: 3.2 mm), broadened at basal 3/5, and markedly narrowed at apical 2/5, slightly directed outward, with apex comparatively wide and subtriangular; median lobe elongate sub-triangular, slightly shorter than the parameres (2.65 mm), apex rounded with an elongate sclerite at mid-line (Fig. 36a, b).

Sexual dimorphism. Females similar to males but with narrow maxillary palpi, third labial palpomere not inflated nor excavated, protibiae with internal spine not truncate, acute, slightly shorter than external. Tarsal claws curved and acute with an acute basal tooth.

Distribution: Costa Rica, Guyana, Mexico: Veracruz, Nicaragua: León, Río San Juan and Venezuela (Arce-Pérez & Morón 2013; Bachmann 1969; Maes 1989) (Distribution in Mexico: Fig. 42).

Taxonomical comments.

This species described from South America has been reported from Mexico and Central America (Arce-Pérez & Morón 2013) as its morphology seems to agree with the original description by Régimbart (1901). Unfortunately, said description is limited, the type material of the species has not been studied thoroughly, and its male genitalia has yet to be described or illustrated. Bachman (1969) recorded the presence of this species in Venezuela but apparently

did not have access to the type specimens. He illustrated the aedeagus of one of the specimens that more closely resembled of *H. (D.) pollens* of *H. (D.) pollens*, rather than that of the specimens from Mexico and Nicaragua that we here identify as *H. (D.) cf. purpurascens* (Fig. 36). The difference between the aedeagus of these species lie at the apex of the parameres which are narrower and convergent in *H. (D.) pollens* while being more robust and sub-parallel in *H. (D.) cf. purpurascens*. The identity of the specimens from Mexico and Nicaragua is here preliminarily attributed to *H. (D.) purpurascens* until the type and additional specimens from all over the Neotropical region are carefully and thoroughly studied.

Key for the species of *Hydrophilus (Dibolocelus)* from Mexico and Central America

Note. The first characters to appear in the couplets are those shared by both sexes when available. However, the best characters for specific identification are those found in male specimens. We recommend following this key with caution if only female specimens that are not associated to males are available.

1. Sixth antennomere long and oval, yellowish brown, almost completely covering the first article of antennal club (Figs. 23, 33); abdominal ventrites with vestiture leaving a slender oval glabrous area at mid-line in ventrite 4 and broader sub-triangular one in ventrite 5 (Figs. 31, 35) in both sexes. Males with robust (inflated) maxillary palpi, third palpomere with a deep broad ventral excavation (Figs. 29, 33), females with narrow palpi, without ventral excavation 2
- 1' Sixth antennomere short and oval, dark brown, not covering the first article of antennal club (Figs. 7, 11, 15, 25); abdominal ventrites with vestiture leaving a wide oval glabrous area at mid-line in ventrites 3–4; and a broader sub-rectangular one in ventrite 5 in both sexes (Figs. 2, 4, 6); males with maxillary palpi narrow (Fig. 25) or slightly flattened towards apex (Figs. 7, 11, 15) in both sexes 3
- 2 (1). Anterior margin of mentum truncated and straight in both sexes (Fig. 33); male genitalia with broad parameres, slightly directed outward, with broad subtriangular apex (Fig. 36 a, b) *H. (D.) cf. purpurascens* Régimbart
- 2' Anterior margin of mentum rounded, unknown female (Fig. 29); male genitalia with parameres comparatively narrow, markedly directed inwards, with slender round apex. (Fig. 32 a, b) *H. (D.) pollens* Sharp
- 3 (1'). 3 (1'). Male with maxillary palpomeres 2 and 3 distinctly flattened and wide towards apex (Figs. 7, 11), slightly flattened in female; male with anterior tibiae internal spur sub-rectangular and with apex truncate (Figs. 8, 12), sub-triangular and acute in female 4
- 3' Male and female with maxillary palpomeres 2 and 3 distinctly slender, only slightly flattened (Figs. 15, 25); males with anterior tibiae internal spur sub-rectangular with apex truncate straight (Fig. 16) or markedly bifid (Fig. 26) 5
- 4 (3). Metaventral spine short, not surpassing the posterior 3/4 of second abdominal ventrite (Figs. 4, 13); third palpomere very wide and flattened with its inner margin slightly curved (Fig. 11). Males with fifth protarsomere somewhat flattened with a small internal laminar expansion, shorter than previous tarsomeres together (Fig. 12); *H. (D.) pseudovatus* sp. nov.
- 4' Metaventral spine long, surpassing the posterior margin of second abdominal ventrite (Figs. 2, 9); third palpomere slightly wide and flat, compared to *H. (D.) pseudovatus*, with its inner margin slightly straight (Fig. 7). Males with fifth protarsomere subcylindrical, without a laminar expansion, longer than previous tarsomeres together (Fig. 8) *H. (D.) ovatus* Gemminger & Harold
- 5 (3') Males with fifth protarsomere as long as the basal together, flat and with evident internal laminar expansion; internal spur of anterior tibiae of males sub-rectangular with apex truncate (Fig. 16) *H. (D.) nucleoensis* sp. nov
- 5' Males with fifth protarsomere shorter than previous tarsomeres together, wide and without internal expansion; internal spur of anterior tibiae of males with bifid apex (Fig. 26) *H. (D.) violaceonitens* Jacquelin du Val

Conclusive remarks

Six species of *Hydrophilus (Dibolocelus)* are found in Mexico (Maps 1-3). One is, so far, known only from Mexico (*H. (D.) pseudovatus* sp. nov.), another is shared with the Nearctic region, and four with the Neotropical region. *Hydrophilus (D.) pseudovatus* sp. nov. is distributed along the Mexican Pacific Coast, the Gulf of Mexico, and Sierra

Madre del Sur; and *H. (D.) pollens* in the Gulf of Mexico province. The three remaining species are found as follows: *H. (D.) violaceonitens* in Mexico (Province of the Gulf of Mexico and Yucatan Peninsula) and the Caribbean (Cuba); *H. (D.) nucleoensis* **sp. nov.** in the Mexican Pacific Coast, Chiapas, Yucatán Peninsula, Eastern Central America and Western Isthmus of Panama provinces; *H. (D.) cf. purpurascens* in the Gulf of Mexico, Chiapas and Eastern Central America provinces (Morrone 2001, Morrone and Márquez 2003). Prior to this work *Dibolocelus* species were known from only seven Mexican states. Here we report their distribution in 15 states. Most localities in Mexico for the species in this subgenus are found in relative low altitude zones. This is probably related the wide distribution of various species throughout the Neotropical region. Such a wide range of distribution conveys difficulties regarding establishing limits for the species and obscure the possibility of synonymy of Mexican species with taxa from Central and South America.

This work is meant to be a taxonomical treatment of the Mexican species that is as comprehensive as possible with the evidence available to us. Nevertheless, different taxonomical questions remain to be answered. Specimens with transitional character states between *H. (D.) ovatus* and *H. (D.) pseudovatus* **sp. nov.** exist in Veracruz and other Mexican states (Andrew E.Z. Short personal communication). Considerable additional collecting in Mexico and genetic analyses are needed in order to understand if they represent zones of hybridization or highly variable species. Also, the real identity of the species here referred as *H. (D.) cf. purpurascens* is yet to be confirmed primarily through comparison with the type specimens and additional specimens from South America. Solving these issues should be the focus of future contributions.

Acknowledgements

We are deeply grateful to the curators of the entomological collections that allowed us to study the material from their institutions. Jean Michel Maes donated the material from Nicaragua to IEXA. We are in debt to Antoine Mantilleri and Christophe Rivier (MNHN) for allowing us to use the pictures of holotype of *H. (D.) violaceonitens*. We especially thank Bruno Clarkson Mattos (Universidade Federal do Rio de Janeiro), Andrew E.Z. Short (University of Kansas) and Martin Fikáček (National Sun Yat-sen University, Taiwan) for their valuable comments that improved the manuscript. J.A. Gómez-Anaya (INECOL) is acknowledged for the help with the habitus pictures of most species. EAV is funded by a posdoctoral grant at the Entomological Collection of the Centro de Estudios en Zoología, Universidad de Guadalajara by CONACyT, Mexico.

References

- Arce-Pérez, R. & Morón, M.A. (2013) El género *Hydrophilus* (Coleoptera: Hydrophilidae: Hydrophilinae) en México y Centroamérica. *Revista Mexicana de Biodiversidad*, 84 (1), 140–152.
<https://doi.org/10.7550/rmb.32113>
- Bachmann, A.O. (1968) Notas sobre Hydrophilini de Venezuela (Coleoptera, Hydrophilidae). *Memoria de la Sociedad de Ciencias Naturales La Salle*, 28 (81), 281–300.
- Bedel, L. (1891) Synopsis des grands Hydrophiles (Genre *Stethoxus* Solier). *Revue d'Entomologie*, 10, 306–323.
- Blackwelder, R.E. (1944) Checklist of the coleopterous insects of Mexico, Central America, The West Indies and South America. Part 1. *Bulletin of the United States National Museum*, 185, i–xii + 1–188.
<https://doi.org/10.5479/si.03629236.185.i>
- Brullé, A. (1837) *Famille des Hydrophiliens. Part. (continued in 1841). In: d'Orbigny, A., Voyage dans l'Amérique méridionale. Vol. 6. Part 2. Insectes. 1836–47.* P. Bertrand, Paris and Strasbourg, pp. 52–56.
- Castelnau, F.L. Laporte de. (1840) *Histoire naturelle des Animaux articulés... Histoire naturelle des Insectes Coléoptères, Vol. 2. Nécropages-Trimères.* P. Duménil, Paris, 565 pp., 38 pls.
<https://doi.org/10.5962/bhl.title.110141>
- Jaqueline du Val, P.N.C. (18457) *Ordre des Coleoptères, Lin. In: Historia física, política y natural de la isla de Cuba. Segunda Parte. Historia Natural. Vol. 7.* A. Bertrand, Paris, pp. 1–868.
- Gemminger, M. & Harold, B. de (1868) *Catalogus Coleopterorum hucusque descriptorum synonymicus et systematicus. Vol. 2.* E. H. Gummi, Monachii [Munich], pp. 425–752 + 6 unnumbered (index).
<https://doi.org/10.5962/bhl.title.9089>
- Geoffroy, E.L. (1762) *Histoire abrégée des Insectes, dans laquelle ces animaux sont rangés suivant un ordre méthodique. Vol. 1.* Durand, Paris, 28 + 523 pp., 10 pls.
<https://doi.org/10.5962/bhl.title.154767>

- Halffter, G. (1987) Biogeography of the montane entomofauna of Mexico and Central America. *Annual Review of Entomology*, 32 (1), 95–114.
<https://doi.org/10.1146/annurev.en.32.010187.000523>
- Halffter, G. & Morrone, J.J. (2017) An analytical review of Halffter's Mexican transition zone, and its relevance for evolutionary biogeography, ecology and biogeographical regionalization. *Zootaxa*, 4226 (1), 1–46.
<https://doi.org/10.11646/zootaxa.4226.1.1>
- Hansen, M. (1991) *The Hydrophiloid Beetles: Phylogeny, Classification, and a Revision of the Genera (Coleoptera: Hydrophiloidea)*. *Biologiske Skrifter* 40. Det Kongelige Danske Videnskabernes Selskab, Copenhagen, 367 pp.
- Hansen, M. (1999) *World Catalogue of Insects. Vol.2. Hydrophiloidea (S.Str) (Coleoptera)*. Apollo Books, Stenstrup and Copenhagen, 416 pp.
- Kuwert, A. (1893) Die grossen Hydrophiliden des Erdballs des Genus *Hydrous* Leach. - *Deutsche Entomologische Zeitschrift*, 1893, 81–93.
<https://doi.org/10.1002/mmnd.48018930113>
- Maes, J.M. (1989) Catálogo de los insectos controladores biológicos en Nicaragua. Volumen II. Insectos depredadores (segunda parte). *Revista Nicaraguense de Entomología*, 9, 1–120.
- Morrone, J.J. (2001) *Biogeografía de América Latina y el Caribe. Manuales y Tesis. SEA. Vol. 3*. Sociedad Entomológica Aragonesa, Zaragoza, 148 pp.
- Morrone, J.J. & Márquez, J. (2003) Aproximación a un Atlas Biogeográfico Mexicano: componentes bióticos principales y provincias biogeográficas. In: Morrone, J.J. & Llorente Bousquets, J. (Eds.), *Una perspectiva latinoamericana de la biogeografía*. Las prensas de Ciencias, Facultad de Ciencias, UNAM, Mexico City, pp. 217–220.
- Régimbar, M. (1901). Revision des grands Hydrophiles. *Annales de la Société Entomologique de France*, 70, 188–232.
- Sharp, D. (1887) *Insecta: Coleoptera. Vol. 1. Part 2. Haliplidae, Dytiscidae, Gyrinidae, Hydrophilidae, Heteroceridae, Parnidae, Georissidae, Cyathoceridae, Staphylinidae*. In: Godman, F.C. & Salvin, O. (Eds.), *Biologia Centrali-Americana. Vol. 16*. Taylor & Francis, London, pp. i–xv + 1–144.
- Short, A.E.Z. (2010) Phylogeny, evolution and classification of the giant water scavenger beetles (Coleoptera: Hydrophilidae: Hydrophilini: Hydrophilina). *Systematics and Biodiversity*, 8, 17–37.
<https://doi.org/10.1080/14772000903529375>
- Short, A.E.Z. & McIntosh, C.E. (2014) Review of the giant water scavenger genus *Hydrophilus* Geoffroy (Coleoptera: Hydrophiloidea) of the United States and Canada. *The Coleopterists Bulletin*, 68 (2), 187–198.
<https://doi.org/10.1649/0010-065X-68.2.187>
- Short, A.E.Z. & McIntosh, C.E. (2015) *Hydrophilus harpe* sp. nov., a remarkable new species of giant water scavenger beetle from Brazil (Coleoptera: Hydrophilidae). *Acta Entomologica Musei Nationalis Pragae*, 55 (2), 665–671.
- Young, F.N. (1954) The water beetles of Florida. *University of Florida Studies, Biological Science Series*, 5 (1), 1–238.
- Smetana, A. (1988) Review of the family Hydrophilidae of Canada and Alaska (Coleoptera). *The Memoirs of the Entomological Society of Canada*, 120 (S142), 3–316.
<https://doi.org/10.4039/entm120142fv>
- Solier, A.J.J. (1834) Observations sur la tribu des Hydrophiliens, et principalement sur le genre *Hydrophilus* de Fabricius. *Annales de la Société entomologique de France*, 3, 299–318.
- Toussaint, E.F., Bloom, D. & Short, A.E.Z. (2017) Cretaceous West Gondwana vicariance shaped giant water scavenger beetle biogeography. *Journal of Biogeography*, 44 (9), 1952–1965.
<https://doi.org/10.1111/jbi.12977>
- Zaitzev, F.A. (1908) Catalogue des Coléoptères aquatiques des familles Dryopidae, Georyssidae, Cyathoceridae, Heteroceridae et Hydrophilidae. *Horae Societatis Entomologicae Rossicae*, 38, 283–420.
- Ziegler, D. (1844) Descriptions of New North American Coleoptera. *Proceedings of the Academy of Natural Sciences of Philadelphia*, 2, 43–47.