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North American Stygobiontic Diving Beetles (Coleoptera: Dytiscidae: Hydroporinae) with Description of *Ereboporus naturaconservatus* Miller, Gibson and Alarie, New Genus and Species, from Texas, U.S.A.

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Abstract

Ereboporus naturaconservatus Miller, Gibson and Alarie, **new genus and new species** (Coleoptera: Dytiscidae) is described from specimens collected from Caroline Springs, Independence Creek, Terrel County, Texas, U.S.A. Specimens were collected using drift nets placed at the head of the spring, suggesting the species is subterranean and occurs in nearby areas of the Edwards-Trinity Aquifer. In addition, the new taxon is characteristic of subterranean diving beetles in having adults depigmented, relatively soft, and lacking metathoracic wings and compound eyes. In addition, the taxon is diagnosed among all adult Dytiscidae in having: 1) the head extremely large relative to the rest of the body, 2) the pronotum short and cordate; 3) the prosternal process small, short and not extending to the mesosternum; 4) the elytra fused along the suture; 5) the elytron and elytral epipleuron extending ventromedially, concealing large lateral portions of the abdominal sterna; 6) the female internal genitalia with a large, elongate, ring-shaped structure on the bursa. The species is placed in the tribe Hydroporini (Hydroporinae) based on the character states: 1) pro- and mesotarsi pseudotetramerous; 2) male genitalia bilaterally symmetrical; 3) scutellum not visible with the elytra closed; 4) prosternum in lateral aspect declivous; 5) metatarsal claws the same length; 6) apices of elytra evenly rounded; 7) metepisternum extending to mesocoxal cavity externally; 8) male lateral lobe with one segment; 9) metacoxal process with well-developed lobes; 10) anterior margin of metafemur distinctly separated from the lobes of the metacoxal process. Three additional subterranean species are known from North America, *Comaldessus stygius* Spangler and Barr, 1995, *Stygoporus oregonensis* Larson and Labonte, 1994, and *Haideoporus texanus* Young and Longley, 1976. Each of these species is figured and discussed.

"Cave or aquifer-adapted aquatic beetles are extremely rare" (Young and Longley 1976). This was thought to be true 30 years ago, but knowledge of these beetles has changed dramatically since then. Until recently, stygobiontic (aquatic subterranean or groundwater adapted) diving beetles (Dytiscidae) were documented only from widely separated geographic areas. Species were sporadically known from New Zealand (Ordish 1976, 1991), Spain (Castro and Delgado 2001), France (Abeille de Perrin 1904), China (Spangler 1996), Thailand (Spangler 1996), Mexico (Franciscolo 1979), Venezuela (Sanfilippo 1958), west Africa (Peschet 1932), and Japan (Uéno 1996; Wewalka *et al.* 2007), in addition to a few species in North America (Young and Longley 1976; Larson and Labonte 1994; Spangler and Barr 1995). With the exception of *Morimotoa* Uéno, 1957 (3 species), *Phreatodessus* Ordish, 1976 (2 species) and *Siettitia* Abeille de Perrin, 1904 (2 species), most of the 13 genera in which these species were placed are monotypic. However, recent discovery of a truly monumental fauna of subterranean dytiscids in western Australia, with about 100 known species in several genera (Watts *et al.* 2007; Leys and Watts 2008), suggests the possibility that underground diving beetles may be more diverse and widespread than previously thought. The Australian diversity has also led to a flurry of interest in exploring their systematics and ecology and associated faunas of other arthropods in these systems and a search for additional faunas in other parts of the world (Watts and Humphreys 1999, 2000, 2004, 2006; Cooper *et al.* 2002; Leys *et al.* 2003; Balke *et al.* 2004; Cooper *et al.* 2007; Watts *et al.* 2007).

The North American fauna of subterranean diving beetles, as currently known, is much less diverse with four species in four genera, including a new one documented here. The purpose of this project is to describe this new genus and species of stygobiontic diving beetle from springs in Texas and review the stygobiontic diving beetle species of North America.

Material and Methods

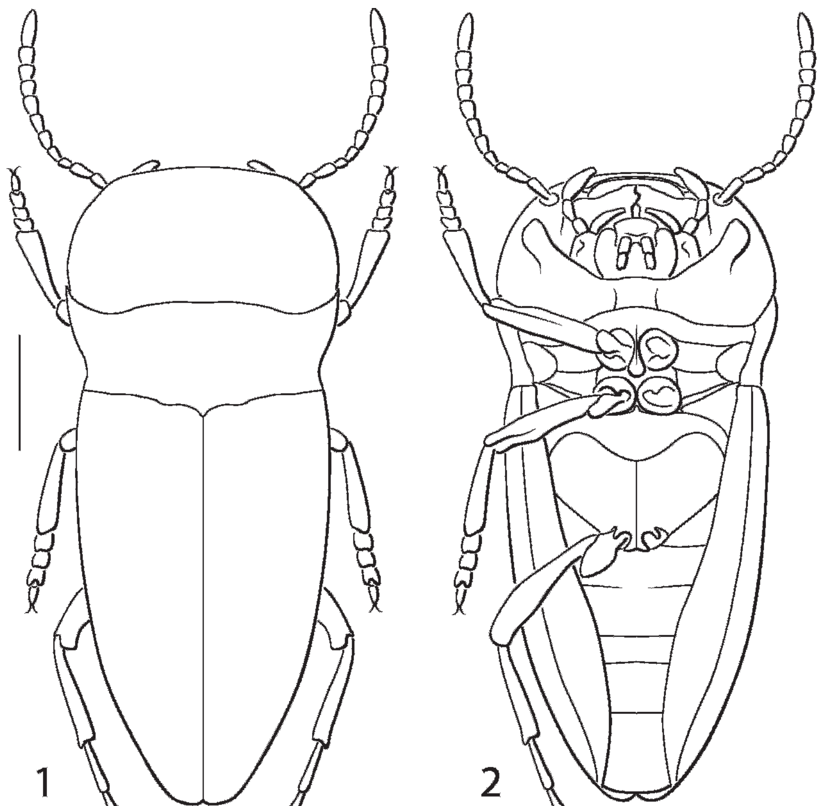
Measurements. Measurements were taken with an ocular scale on a Wild M3C dissecting microscope. Measurements include: TL = total length; HL = length of head along midline; HW = greatest width of head; PL = length of pronotum along midline; PW_1 = greatest width of pronotum; PW_2 = minimum width of pronotum; EL = length of elytron along midline; EW = greatest width across both elytra; FL = greatest length of metafemur; RL = greatest length of metatrochanter. Ratios are also provided to give an indication of shape or proportion.

Material. This project is based on three specimens collected in drift nets (300–500 μm) over two spring orifices of Caroline Springs, the headwaters of Independence Creek, Terrell County, Texas. The holotype and one paratype are deposited in the Division of Arthropods, Museum of Southwestern Biology, University of New Mexico, Albuquerque, New Mexico, U.S.A. (MSBA, K.B. Miller, curator). From this paratype, DNA was extracted and deposited in the MSBA. The second paratype is deposited in the United States National Museum, Smithsonian Institution (USNM). Specimens of *Haideoporus texanus* Young and Longley and *Comaldessus stygius* Spangler and Barr were also collected (at Comal Springs, a different locality from the new species) and the DNA extracted with the intention of using these DNAs for an analysis to place these species in the phylogeny of the Hydroporinae. Vouchers and DNAs of these specimens are also deposited in the MSBA.

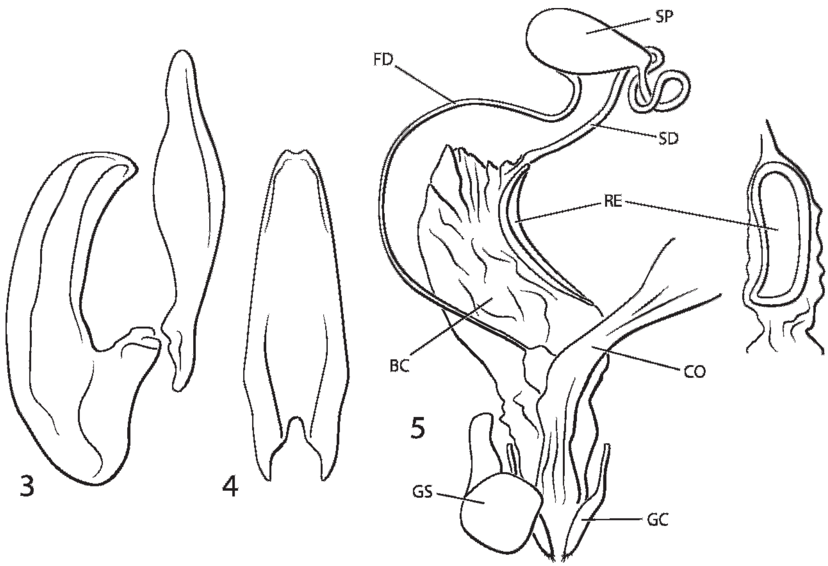
Ereboporus Miller, Gibson and Alarie, new genus
(Figs. 1–5, 17)

Type Species. *Ereboporus naturaconservatus* **new species** by present designation.

Diagnosis. Adults of this genus are unique among Hydroporinae in having the following character combination: 1) eyes absent (Figs. 1, 2); 2) head very broad with body widest at head (Figs. 1, 2); 3) pronotum broadest anteriorly, conspicuously constricted medially (Figs. 1, 2); 4) body depigmented and weakly sclerotized; 5) elytra fused along suture; 6) metathoracic wings absent; 7) prosternal process short, apex round, not extending between mesocoxae to metasternum (Fig. 2); 8) elytral epipleuron broad throughout length, extending ventrally to cover significant portions of lateral regions of metacoxae and abdominal sterna (Fig. 2). The genus is similar in general shape to other cave-adapted Dytiscidae, especially *Morimotoa*, but these seem likely to be



Figs. 1–2. *Ereboporus naturaconservatus*, habitus. **1**) dorsal aspect; **2**) ventral aspect. Scale bar = 0.5 mm.



Figs. 3–5. *Ereboporus naturaconservatus*. **3**) male genitalia, right lateral aspect; **4**) male median lobe, ventral aspect; **5**) female genitalia. BC = bursa copulatrix, CO = common oviduct, FD = fertilization duct, GC = gonocoxa, GS = gonocoxosternite, RE = receptacle, SD = spermathecal duct, SP = spermatheca.

convergences due to similar adaptations to living in a subterranean environment. The most distinctive features in *Ereboporus* distinguishing the genus from similar genera are the dramatically large head and broad anterior margin of the pronotum, the longitudinally short pronotum, and the broad elytral epipleuron which extends ventromedially covering much of the lateral margins of the thoracic and abdominal sterna (Figs. 1, 2). The male genitalia are relatively simple with the median lobe robust and curved dorsad (Figs. 3, 4). The lateral lobe is narrow (Fig. 3). The female genitalia are unique in having elongate, slender spermathecal and fertilization ducts, a small spermatheca, and an apparent structure homologous with the receptacle (Miller 2001) in the form of an elongate ring-like structure on the right lateral surface of the bursa (Fig. 5; see Discussion below).

Etymology. The genus is named *Ereboporus* from the Greek, *Erebos*, meaning "hell," and *–porus*, a common root for genus names in the subfamily Hydroporinae.

Distribution. Specimens of the single species in this genus were recovered in the flow at the head of Caroline Springs in Terrell County, Texas. These springs emerge from the Edwards-Trinity Aquifer, a portion of the larger Edwards-Trinity Aquifer system which covers an area of 200,000 km^2 across Texas (Ryder 1996, Fig. 17). Whether *E. naturaconservatus* occurs throughout this aquifer, in other aquifers, or in only a small area associated with this spring is unknown.

Discussion. The genus is placed in the tribe Hydroporini (Hydroporinae) based on the characters: 1) pro- and mesotarsi pseudotetramerous (Fig. 2); 2) male genitalia bilaterally symmetrical (Fig. 4); 3) scutellum not visible with the elytra closed (Fig. 1); 4) prosternum in lateral aspect declivous; 5) metatarsal claws the same length; 6) apices of elytra evenly rounded (Fig. 1); 7) metepisternum extending to mesocoxal cavity externally (Fig. 2); 8) male lateral lobe with one segment (Fig. 3); 9) metacoxal process with small, but well-developed lobes (Fig. 2); 10) anterior margin of metafemur distinctly separated from the lobes of the metacoxal process (Fig. 2).

Placement of stygobiontic diving beetles can be problematic since they are often so highly apomorphic but with features convergent with other stygobiontic taxa. This combination of attributes has resulted in numerous monotypic genera of stygobiontic diving beetles. In several cases, evidence (in some cases molecular evidence) indicates that stygobiontic taxa are, in fact, nested within genera among species that occur in more typical habitats (Leys *et al.* 2003; Leys and Watts, 2008; Wewalka *et al.* 2007). Thus, there exists the possibility that this new species belongs to a described genus. We think this is unlikely, even in the absence of a cladistic test, in large part because of the unique female genitalia. These are unusual in several respects. Most conspicuously, the bursa has an elongate ring-like structure on the right side that we hypothesize to be homologous with the receptacle found in other Hydroporinae (Miller 2001). This structure in other hydroporines often has a sclerotized ring around its base (Miller 2001), similar to the ring-shaped structure on the bursa of *Ereboporus* and at least some groups have the receptacle on the bursa (*e.g.*, *Porhydrus* Guignot, Miller *et al.* 2006). It is not clear how this structure functions in hydroporines or how the particular modification of this structure functions in *Ereboporus*. The other taxa with the receptacle on the bursa are not particularly similar to *Ereboporus* in other characters, nor are they similar to each other. Because of the uniqueness of this particular character system in this new species, we are relatively confident in our placement of it in its own genus. In any case, were we to place this new species in an existing genus, we are not sure which one, and any placement would require expansion of an existing genus circumscription, an undesirable situation. Naturally, we would welcome evidence from a future investigation (such as from a comprehensive cladistic analysis we are currently undertaking) that more convincingly places this unique taxon among the genera of Hydroporini.

***Ereboporus naturaconservatus* Miller, Gibson and Alarie, new species**
(Figs. 1–5, 17)

Type Locality. United States of America, Texas, Terrell County, Independence Creek Nature Conservancy Preserve, Caroline Springs.

Diagnosis. This is the only member of the genus known and is characterized by the diagnostic combination unique to the genus (see above).

Description. *Measurements* (in mm). TL= 2.3–2.4; TL/GW = 2.2–2.4; HL = 0.7; HW = 1.0; HL/HW = 0.7; PL = 0.4; PW_1 = 1.0–1.1; PW_2 = 0.8–0.9; PL/PW_1 = 0.4; PW_1/PW_2 = 0.8–1.2; EW = 0.9; EL=1.4; FL = 0.6; RL = 0.2; RL/FL = 0.3.

Habitus. Body elongate, greatest body width at head, dorso-ventrally depressed; body lightly sclerotized; coloration yellow over entire body.

Sculpture and structure. Head (Figs. 1, 2) very large in proportion to body (L/W); eyes absent; anterior margin of clypeus concave, with continuous marginal bead; length of scape and pedicel each about 2× width; length of flagellomeres I–VIII about 1.2× width, apical flagellomere length about 2.5× width. Pronotum (Figs. 1, 2) short and broad, greatest width anteriorly; anterolateral corners sharply pointed, extending anteriorly along lateral margins of head; submedially prominently constricted; posterolateral corners acute. Scutellum not externally visible. Elytron (Figs. 1, 2) elongate, elytra medially weakly fused along elytral suture, though not strongly so; lateral margin evenly and broadly curved anteriorly, elytra together slightly tapered posteriorly; elytral epipleuron very broad throughout length, extending medially, covering significant portions of lateral areas of metacoxae and abdominal sternites. Metathoracic wings absent. Head, pronotum, and elytron covered with microsculpture composed of fine, isodiametric cells making surface matte in appearance. Prosternum (Fig. 2) narrow; prosternal process very small, apically rounded, length about equal to width, not extending between mesocoxae to metasternum. Metacoxa (Fig. 2) large; metacoxal lines absent; apical lobes of posterior metacoxal process short and rounded; metacoxal bridge not differentiated (posterior margin of metacoxal process without delimiting margin), medially evenly sloped to abdomen; metatrochanter (Fig. 2) large, distinctly offset from metafemur, apex bluntly pointed, remote from metafemur; metafemur (Fig. 2) slender and elongate; metatibia (Fig. 2) slender, slightly and gradually expanded apically. Visible abdominal sternites II and III fused with suture absent medially (Fig. 2). Conspicuous sensory setae absent over entire body. Series of spinous setae present only on legs, but natatory setae entirely absent.

Male genitalia. Median lobe in lateral aspect (Fig. 3) short, robust, broad, apex abruptly curved dorsad, apically broadly pointed; in ventral aspect (Fig. 4) broad, lateral margins evenly convergent to apex which is distinctly but shallowly emarginate. Lateral lobe (Fig. 4) relatively narrow, medially expanded, apex rounded.

Female genitalia. Gonocoxosternite (Fig. 5) with posterior portion rhomboid, anterior portion elongate, moderately broad, slightly curved medially near anterior end; gonocoxa (Fig. 5) elongate, slender, medially bent; bursa copulatrix (Fig. 5) elongate, anteriorly broadly expanded, with elongate ring-like sclerotized structure on right side (receptacle); spermathecal duct (Fig. 5) elongate, slender; spermatheca (Fig. 5) robust, expanded on end near fertilization duct; fertilization duct (Fig. 5) elongate, slender.

Etymology. The species name, *naturaconservatus*, comes from the Latin words *natura*, meaning "nature" and *conservatus*, meaning "keep" or "conserve," in honor of The Nature Conservancy for their extensive work in the promotion of biodiversity and specifically in honor of the Independence Creek Nature Conservancy Preserve, the type locality for the species.

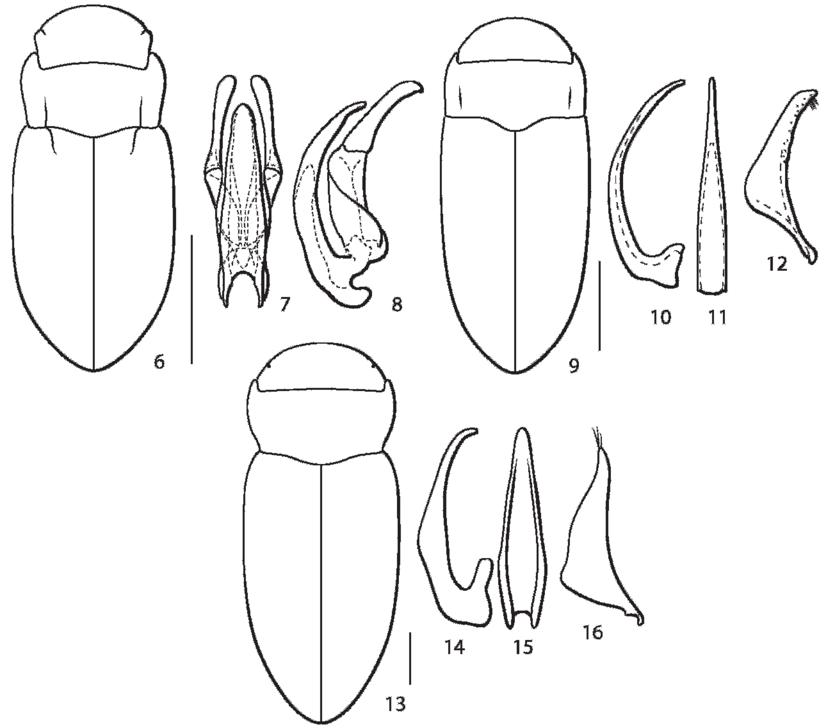
Distribution and Habitat. Same as for the genus (see above).

Material Examined. Holotype: ♂ labeled, "U.S.A.: Texas, Terrell Co., Independence Creek Preserve, Caroline Springs, 24.3 km S Sheffield, 30°27′10″N 101°44′10″W, 19 May 2007, J.R. Gibson and E. Chappell, colrs./ HOLOTYPE: Miller, Gibson and Alarie, 2008 [red label with double black line border]." **Paratypes**: 2 labeled same as holotype except "/PARATYPE: Miller, Gibson and Alarie, 2008 [blue label with black line border]."

Other subterranean Dytiscidae in North America

Comaldessus stygius Spangler and Barr, 1995
(Figs. 6–8)

Comaldessus stygius Spangler and Barr 1995: 302; Nilsson 2001: 119; Larson *et al.* 2000: 101.



Figs. 6–16. Subterranean Dytiscidae. **6–8**) *Comaldessus stygius*, **6**) dorsal habitus, **7**) male genitalia, ventral aspect, **8**) male genitalia, right lateral aspect. **9–12**) *Stygoporus oregonensis*, **9**) dorsal habitus, **10**) male median lobe, right lateral aspect, **11**) male median lobe, ventral aspect, **12**) male right lateral lobe, right lateral aspect. **13–16**) *Haideoporus texanus*, **13**) dorsal habitus, **14**) male median lobe, right lateral aspect, **15**) male median lobe, ventral aspect, **16**) male right lateral lobe, right lateral aspect. Scale bar = 0.5 mm.

Type Species. *Comaldessus stygius* Spangler and Barr, 1995 by original designation.

Type Locality. U.S.A., Texas, Comal County, New Braunfels, Landa Park, Comal Spring #3.

Diagnosis. This species can be distinguished from other taxa within Bidessini using the following character combination: 1) eyes rudimentary, indicated by only a few ommatidia; 2) metacoxal lines absent; 3) occipital line absent (Fig. 6); 4) basal pronotal and basal elytral striae ("plicae") present (Fig. 6).

Discussion. *Comaldessus stygius* was described from twelve specimens collected in drift nets from Comal Springs (Spangler and Barr 1995), a system of artesian springs.

Relationships. This species is clearly a member of the tribe Bidessini based on the 2-segmented parameres (Biström 1988) and the presence of basal pronotal and elytral striae (Fig. 6) which are characteristic of many Bidessini (Biström 1988). Spangler and Barr (1995) speculated that the species is related to *Trogloguignotus* Sanfilippo and *Uvarus* Guignot and that both *Trogloguignotus* and *Comaldessus* are derived from within the species-rich, plesiomorphic *Uvarus*, though without a

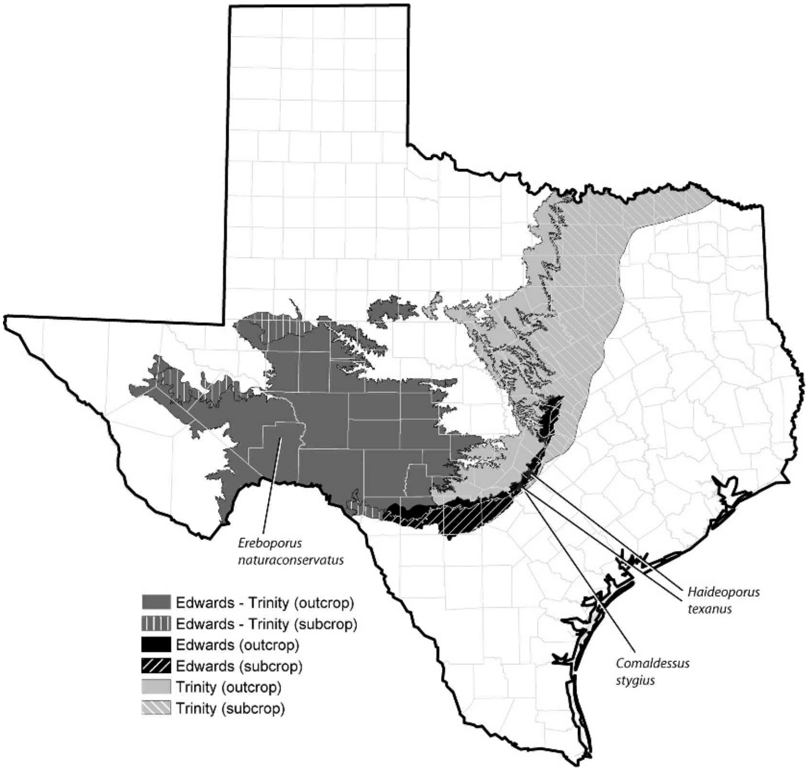


Fig. 17. Map of state of Texas, U.S.A. showing extent of several related aquifer systems and known distribution of *Comaldessus stygius*, *Haideoporus texanus* and *Ereboporus naturaconservatus*.

cladistic analysis of this problematic tribe, it is difficult to make definitive conclusions.

Stygoporus oregonensis Larson and Labonte, 1994
(Figs. 9–12)

Stygoporus oregonensis Larson and Labonte 1994: 371; Nilsson 2001: 189; Larson *et al.* 2000: 138.

Type Species. *Stygoporus oregonenesis* Larson and Labonte, 1994 by original designation.

Type Locality. U.S.A., Oregon, Polk County, 7 km NNE Dallas, Smithfield Road, 44.973°N, 123.275°W, 90 m, well.

Diagnosis. This species is unique within Hydroporini in having the following combination of characters: 1) compound eyes absent; 2) prosternal process inserted dorsad of the anterior margin of the metasternum; 3) with longitudinal impressions laterally on the pronotum (Fig. 9); 4) metacoxal processes together truncate posteriorly; 5) with natatory setae on the metatarsus and metatibia.

Discussion. This species was described from nine specimens collected from a shallow well. The owners of the well, thinking the beetle may be a pest, chlorinated the well and the species has not been seen since (Larson and Labonte 1994). Larson and Labonte (1994) suggested that the presence of specimens in this particular well (an old well with no previous indication of a diving beetle fauna) may have been the result of an unusually large amount of precipitation that year in the region, possibly resulting in a change in the nature of the aquifer and temporarily allowing beetles into the well.

Relationships. Larson and Labonte (1994) speculated that *Stygoporus* is the sister group to *Sanfilippodytes* Franciscolo based on the enlarged metatrochanters and produced posterior margin of the medial portions of the metacoxa. *Sanfilippodytes* occur in seeps and springs, and seem to be a likely candidate for occurrence in underground waters. One species, *S. sbordonii* Franciscolo, was described from a cave in Mexico (Franciscolo 1979). Although not anophthalmic like *Stygoporus*, *S. sbordonii* does have smaller eyes than typical *Sanfilippodytes* (Larson and Labonte 1994).

Haideoporus texanus **Young and Longley, 1976**
(Figs. 13–16)

Haideoporus texanus Young and Longley 1976: 788; Longley and Spangler 1977: 532 (description of larvae); Bowles 1997: 297 (new distribution records); Nilsson 2001: 152; Larson *et al.* 2000: 138.

Type Species. *Haideoporus texanus* Young and Longley, 1976 by original designation.

Type Locality. U.S.A., Texas, Hays County, San Marcos, Southwest Texas State University, Aquatic Station, artesian well.

Diagnosis. *Haideoporus texanus* can be distinguished from other Hydroporini by the following: 1) eyes small, located anterolaterally on head; 2) setae of body and legs extremely long; 3) pro- and mesocoxae large, globular; 4) prosternal process not extending posteriorly between mesothoracic legs to mesosternum.

Discussion. This species was discovered in a well on the campus of Texas State University in San Marcos, Hays County, Texas (Young and Longley 1976) and subsequently also found at Comal Spring, Comal County, Texas (Bowles and Stanford 1997), the type locality for *C. stygius* (see above). The larva of *Haideoporus* has been described (Longley and Spangler 1977), making it the only subterranean dytiscid larva from North America described to date.

Relationships. The species is currently placed in the Hydroporini (Nilsson 2001), but Young and Longley (1976) were cautious to make definitive statements about the relationships of this species to others in its subfamily. They pointed out close similarities of *Haideoporus* with other subterranean diving beetles, such as *Morimotoa* and *Siettitia*, but suspected that these similarities were due to convergence in similar habitats.

Discussion

In addition to *E. naturaconservatus*, the springs of the Edwards and Trinity Aquifer Systems in central and western Texas have yielded two stygobiontic diving beetle species, *H. texanus* and *C. stygius*. The presence of several species in groundwaters in Texas is tantalizingly suggestive of the diversity of the fauna found in Western Australia. This fauna in Australia went unnoticed until bore holes and wells drilled into the aquifers allowed access throughout the region

(Watts and Humphreys 1999). An additional Nearctic subterranean species, *S. oregonensis*, is known from Oregon, U.S.A. Knowledge of whether a similar diverse fauna exists in North American aquifers may have to wait until better means for accessing and sampling the habitat becomes available.

As pointed out by Franciscolo (1983) and reviewed by Spangler (1996), Larson and Labonte (1994), and Watts and Humphreys (1999), subterranean Hydradephaga possess a suite of presumably convergent character states, some of which are typical of subterranean arthropods including: 1) microphthalmy or anophthalmy; 2) depigmentation; 3) desclerotization of the exoskeleton; 4) wings absent; 5) general "frailty." Many (though not all) subterranean diving beetles also possess characteristics particularly unique within Dytiscidae, including: 1) the natatory setae on the legs reduced and correlated with a presumably reduced swimming ability; 2) a medially constricted pronotum (*e.g.*, Fig. 1); 3) the prosternal process short, not extending between the mesocoxae to the anterior margin of the mesosternum (Fig. 2). These features, which are certainly evident in *Ereboporus* and the other species of North American subterranean diving beetles, occur sporadically throughout the Dytiscidae. As discussed by Larson (1991), the second and third of these states, at least, are characteristic of rheophilic and hyporheic beetles. Presumably, the medially constricted pronotum combined with a shortened prosternal process improves maneuverability by allowing greater flexibility at the prothorax-mesothorax interface. Such modifications may allow the beetle to move better among interstices.

Acknowledgments

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