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Revision of the Genus *Eretes* Laporte, 1833 (Coleoptera: Dytiscidae)

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Abstract

The genus *Eretes* Laporte is revised. Four species are recognized in the genus; 1) *E. australis* (Erichson) (= *E. punctipennis* (MacLeay)), 2) *E. griseus* (Fabricius) (= *E. plicipennis* (Motschulsky), = *E. succinctus* (Klug), = *E. moroderi* Báguena Corella), 3) *E. sticticus* (Linnaeus) (= *E. punctatus* (Zoubkoff), = *E. helvolus* (Klug), = *E. occidentalis* (Erichson), = *E. conicollis* (Wollaston), = *E. subcoriaceus* (Wollaston), = *E. subdiaphanus* (Wollaston)) and 4) *E. explicitus* Miller, sp. n. The taxonomic history of the group is reviewed. The tribe and genus are diagnosed and a key to the species is provided. Each species is diagnosed, its general distribution is provided and important morphological features are illustrated. The larva of *E. australis* is illustrated and used to diagnose the tribe. Evidence for the sister-group relationship between Eretini and Aciliini and for relationships within the tribe is presented based on characters from adult and larval morphology.

Keywords: *Eretes*, diving beetles, taxonomy, nomenclature.

Introduction

Eretes Laporte has a long and complicated taxonomic history as is partially indicated by the abundance of species-group names associated with the genus. For over 100 years, the genus has been considered by most workers to comprise two species, *Eretes australis* (Erichson), from Australia and Tasmania, and *E. sticticus* (Linnaeus), from much of the rest of the world. After examining numerous series of specimens it became clear to me that more than just two species exist. However, the complex collection of names attributed to the genus, mostly regarded as junior synonyms of *E. sticticus*, did not allow a confident assignment of names to specimens, thus stimulating this revision.

The early history of the nomenclature of this genus is particularly confusing. The generic concept, under the name *Eunectes* Erichson, was established to include the

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species *Dytiscus sticticus* Linnaeus with a single junior synonym *D. griseus* Fabricius. After this, the genus underwent nomenclatural changes since *Eunectes* Erichson was preoccupied by *Eunectes* Wagler (Reptilia). *Nogrus*, a name which appeared first in the Dejean (1833) catalog, was apparently intended to be a replacement name. *Nogrus* was attributed to Eschscholtz by Dejean (1833), but the name was never published by Eschscholtz (Neave, 1939). Neave (1939) regarded *Nogrus* as a *nomen nudum*. However, since the name was introduced in combination with available species names, the name is available by indication (Article 12.2.5 of the Zoological Code). Early catalogs often attribute the name to Eschscholtz, but because it was published first by Dejean (1833) the name is correctly attributed to him. *Eretes* Laporte (1833) was erected the same year as *Nogrus* but with a different type species.

The generic nomenclatural changes were further confused as subsequent authors used various names when introducing or cataloging species, varieties or aberrations. For example Aubé (1838) recognized *Eunectes* as valid with *Eretes* and *Nogrus* as synonyms, though he regarded *Nogrus* as an unpublished name attributed to Eschscholtz. Gemminger and Harold (1868) accepted *Eunectes* as valid and recognized ten species. Most authors continued to use the genus name *Eunectes* and no less than eleven species, varieties or aberrations were described under that name. The name *Eretes* eventually became more generally used subsequent to its use as the valid name by Crotch (1873), Régimbart (1878) and Sharp (1882). Even so, as late as 1929 *Eunectes* was (invalidly) used as the type genus of the tribe Eunectini Portevin (1929).

Members of this genus are extremely diverse in size, shape and color pattern. Early authors used these characters to delimit species. As in many other Dytiscidae, and in *Eretes* in particular, these features are not particularly useful since the variation overlaps extensively between and within populations. Sharp (1882) regarded these differences as trivial and recognized only *E. australis* and *E. sticticus*. Male genitalia have been relatively little used in this group. However, Gschwendtner (1954) made a detailed study of male genitalia and other characters mainly in an attempt to name the species present in Peru. He came to similar conclusions regarding species circumscriptions as I have in this study. However, his nomenclatural conclusions differ dramatically from mine, and he did not attempt to sort out much of the nomenclatural morass associated with the genus. Subsequent authors (e.g., Guignot, 1961) did not adopt Gschwendtner's classification of the group. Recently, questions regarding the number of species and their distributions have arisen again (e.g., Larson et al., 2000).

Eretes individuals have very short larval and pupal stages (Kingsley, 1985; Nowrojee, 1912). Larvae feed on a variety of small crustaceans and small insects, including other *Eretes* larvae (Kingsley, 1985). Adults feed on various animal material such as insect larvae or pieces of dead fish (Swamy & Rao, 1974). *Eretes* are often associated with desert environments or other areas with ephemeral water sources where, with their fast development, they can exploit the short-lived resources. They are exceptional dispersers and can be found in small, very isolated pools far from other aquatic habitats, blacklight samples in dry environments, and many remote islands. Kingsley (1985), Nowrojee (1912) and Swamy and Rao (1974) provide a variety of additional life history information.

With no less than three genus-group and 17 species-group names associated with this taxon, my primary goals in this paper are to hypothesize the number of species and clarify the taxonomy of the available names based on a critical examination of discrete characters emphasizing male and female genitalic characters and examination of type specimens. I also diagnose and key the species, provide general distribution information, describe a species of *Eretes* new to science, and present evidence for the phylogeny of the group.

Material and Methods

Material. A truly vast number of specimens of this genus exist in collections. Attempting to assemble and examine all of these specimens would be an unreasonable task. Instead, specimens were borrowed from a few collections in North America, Africa and Europe. Even so, many hundreds of specimens were examined, enough to assess the species limits, variation and the general distribution. Emphasis was placed on examination of the numerous type specimens for the available names in the genus and dissection of males and females from a broad greographic range. Several hundred males and females were dissected to examine genitalia. Specimens were examined from the following collections; Australian National Insect Collection, Canberra, T.A. Weir (ANIC); The Natural History Museum, London, S. Hine (BMNH); Cornell University Insect Collection, Comstock Hall, Cornell University, Ithaca, J. Leibherr (CUIC); Museum für Naturkunde der Humboldt-Universität, Berlin, M. Uhlig (MNHU); Naturhistorisches Museum, Vienna, Austria, M. Balke (NMWC); National Museum of Namibia, Windhoek, Namibia, A.H. Kirk-Spriggs (SMWN); National Museum of Natural History, Washington, DC, P. Spangler (USNM); Universitetes Zoologiske Museum, Copenhagen, Denmark (ZMUC); and Zoological Museum, University of Helsinki, Finland, O. Biström (ZMUH).

Literature. There are a very large number of papers referring to these species such that a complete bibliography would fill volumes. In presenting bibliographies, I have focused mainly on papers with taxonomic changes and significant catalogs treating the entire family or order rather than isolated references to particular species or regional treatments except for large, select faunal monographs.

Descriptions. A complete description applying to all species is provided under the treatment of the tribe, but only shorter diagnoses and comments on variation are provided under the treatments of the species. The third instar larva of *Eretes australis* is the only species for which I have examined larval specimens, but as it appears similar to published descriptions of larvae of members of the group (Bertrand, 1949; 1972; Mayet, 1887; Meinert, 1901) its characters are used to diagnose larvae for the tribe.

Measurements. Several measurements were made using a digital micrometer attached to a Wild M3C dissecting microscope at 12.6–40.0× magnification including total length (TL), greatest width (GW), greatest width of pronotum (PW), greatest width of head (GW), distance between eyes (EW), medial length of pronotum (PL) and medial length of elytron (EL). Several ratios of these measurements are provided to give an indication of shape for some structures. For adults, the range, mean and standard deviation are provided for ten individuals from each sex. For larvae of *E. australis*, seven individuals were measured.

Figures. Illustrations were made using drawing tubes on a Wild M3C dissecting microscope and on a Leitz Dialux 20 compound microscope. Sketches were scanned and digitized and plates were made using bitmap and vectored image editing software.

Taxonomy

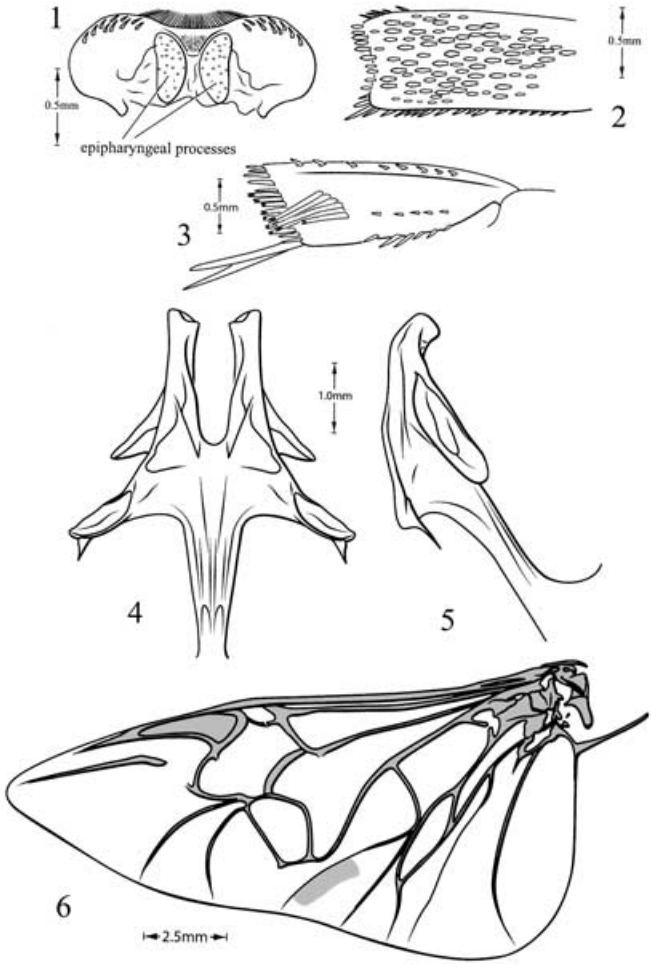
Eretini Crotch, 1873

Eretini Crotch, 1873 (erected as tribe of Dytiscides: type genus, *Eretes* Laporte, 1833); Leng, 1920 (as tribe of Hydaticinae); Nilsson et al., 1989.

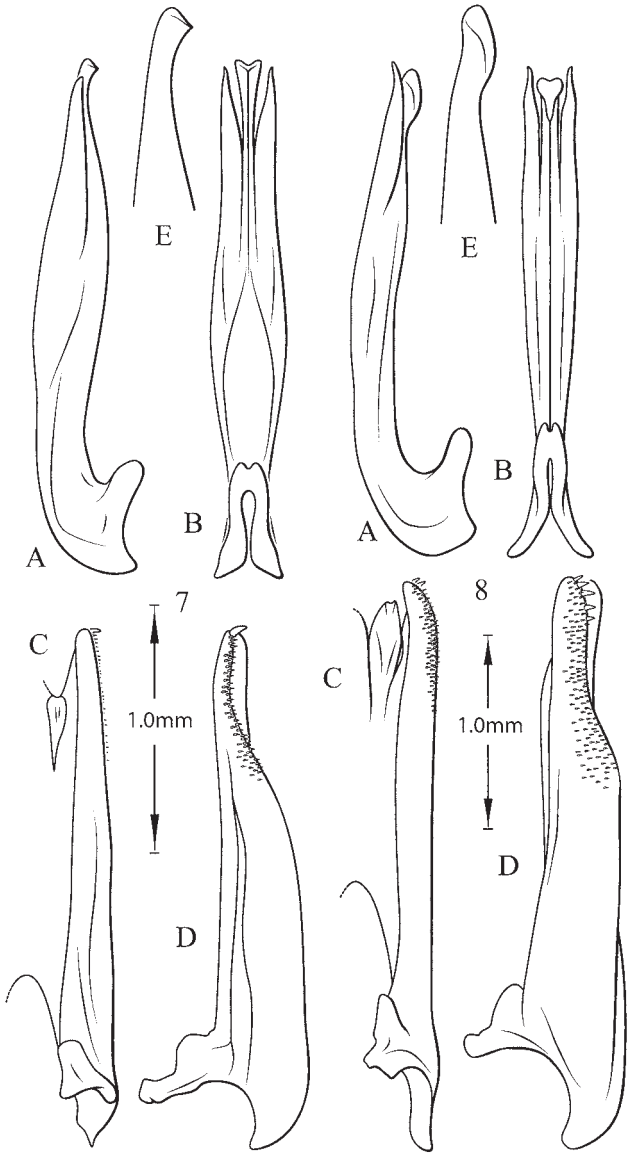
Eunectini Portevin, 1929 (erected as tribe of Dytiscinae: type genus, *Eunectes* Erichson, 1832: invalid as the type genus is a junior homonym).

Diagnosis

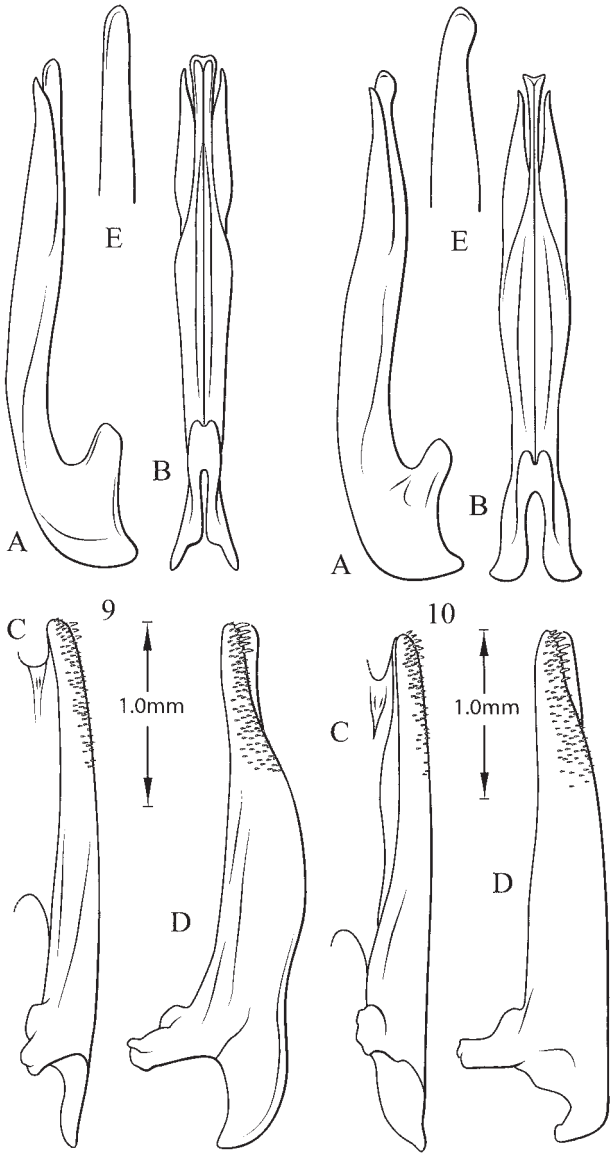
Adult. Prosternal process apically narrow and sharply pointed; pronotum with narrow lateral bead; surfaces of meso- and metatarsomeres with adpressed, flattened setae (Fig. 2); posterolateral margin of elytron with linear series of short, curved spines; elytra very thin and flattened and relatively lightly sclerotized overall; elytra punctate with each puncture bearing a black spot; pale-colored on all surfaces with small to extensive black markings on the dorsum of the head, pronotum and elytra (Figs. 15–23); and epipharyngeal processes very large, oval and flattened (Fig. 1).



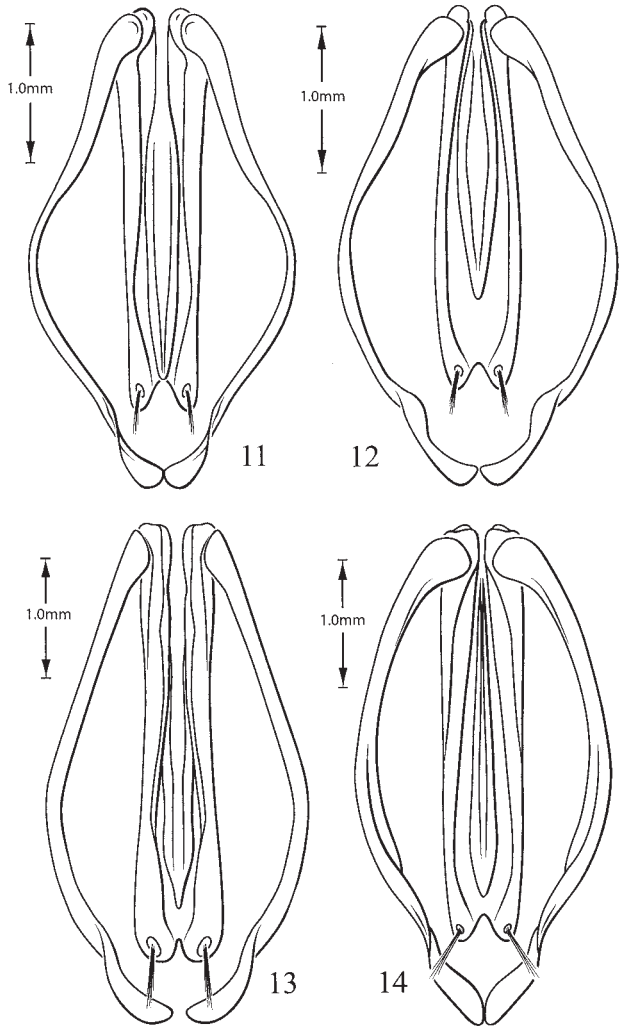
Figures 1–6. *Eretes* species. (1) Labrum and epipharynx, ventral aspect showing epipharyngeal processes. (2) Right metatarsomere one, anterior aspect. (3) Left metatibia, posterior (dorsal) aspect. (4–5) Metendosternite: (4) dorsal aspect; (5) lateral aspect. (6) Left metathoracic wing.



Figures 7–8. Male genitalia, *Eretes* species. (7) *E. australis*. (8) *E. griseus*. (A) Median lobe, right lateral aspect. (B) Median lobe, ventral aspect. (C) Left lateral lobe, ventral aspect. (D) Left lateral lobe, left lateral aspect. (E) Apex of medial portion of median lobe, right lateral aspect. Scale bars for A–D only.

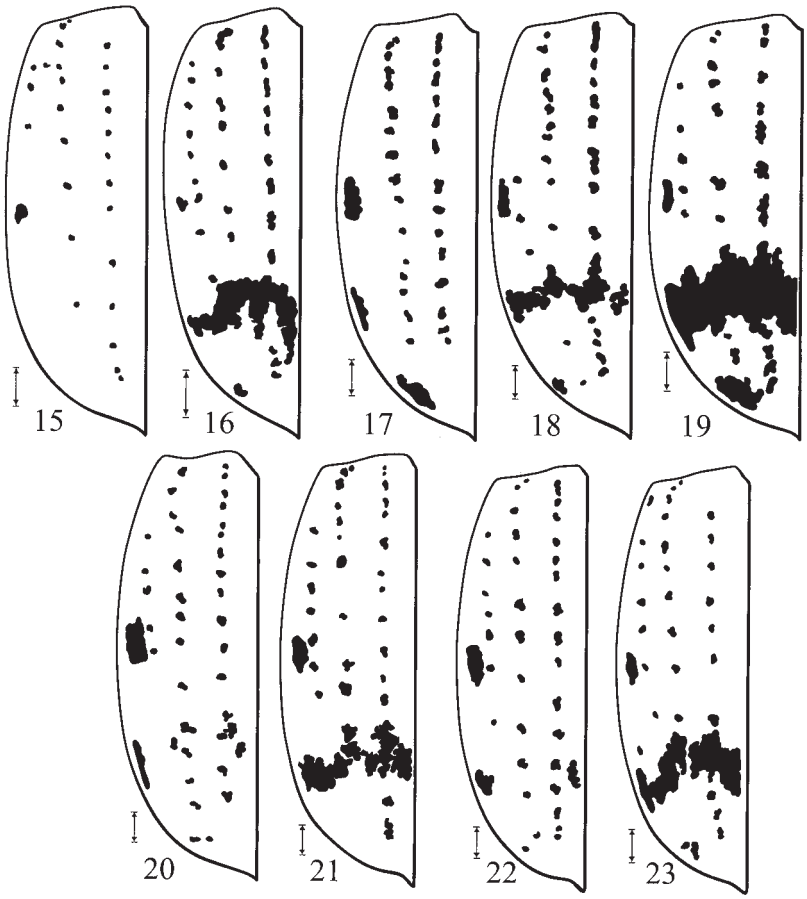


Figures 9–10. Male genitalia, *Eretes* species. (9) *E. sticticus*. (10) *E. explicitus*. (A) Median lobe, right lateral aspect. (B) Median lobe, ventral aspect. (C) Left lateral lobe, ventral aspect. (D) Left lateral lobe, left lateral aspect. (E) Apex of medial portion of median lobe, right lateral aspect. Scale bars for A–D only.



Figures 11–14. Female genitalia; gonocoxae, rami and laterotergites, *Eretes* species. (11) *E. australis*. (12) *E. griseus*. (13) *E. sticticus*. (14) *E. explicitus*.

Third instar larva. Anterodorsal two stemmata larger than others and directed dorsally (Figs. 24, 25); anterior margin of labium with distinct median lobe or process, apically with four stout spinous setae (Fig. 29); with bifid setae along anterior margin of clypeus; body able to bend characteristically in middle and with distinctive swimming behavior achieved by rapid flexing and extension of the body (Fig. 24); stipes of maxilla broad, medial margin with series of spinous setae, lateral margin with series of fine, elongate setae, apicolaterally (near base of palpus) with one or two fine, spatulate setae, galea elongate with dorsal and ventral series of spinous



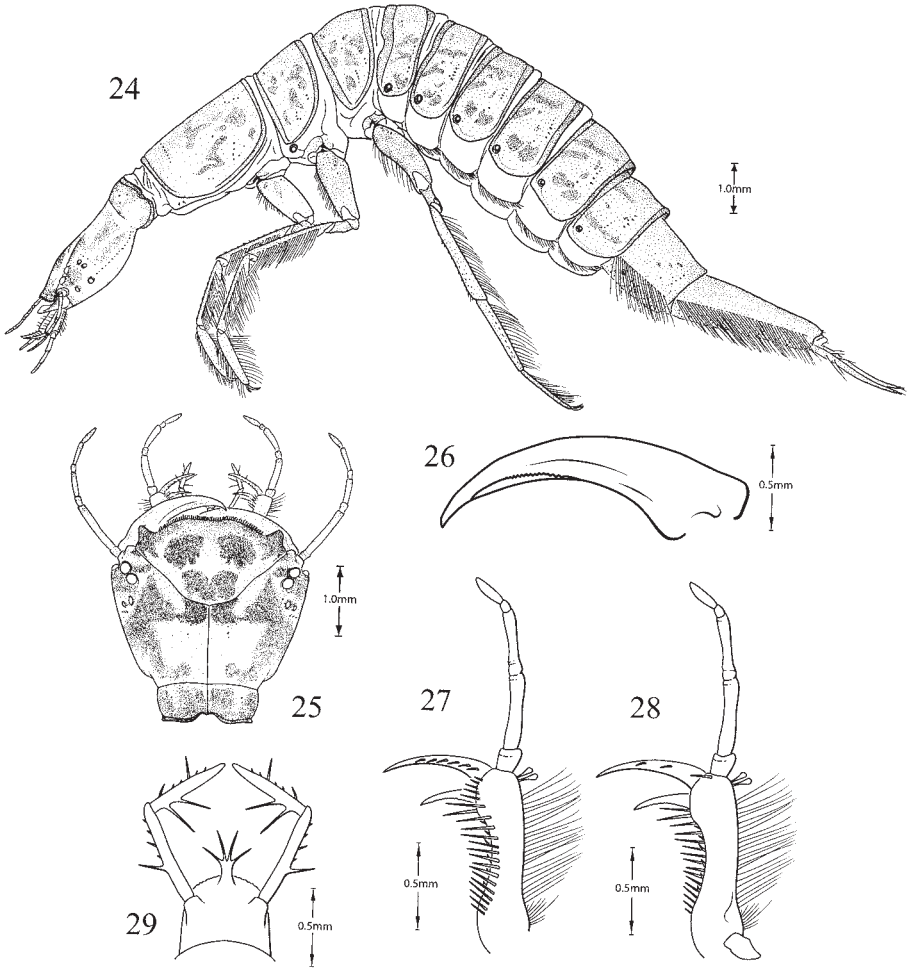
Figures 15–23. Left elytron, *Eretes* species showing variation in extent of black maculation. (15–16) *E. australis*. (17–19) *E. griseus*. (20–21) *E. sticticus*. (22–23) *E. explicitus*.

setae, lacinia present, elongate, acute (Figs. 27, 28). Selected measurements in Table 3 below.

Description

Coloration. Color of nearly all sclerites light yellow; with variably sized black maculae medially along posterior margin of head; elytron with very many small, black maculae, each set at puncture, black maculae variably confluent, especially at lateral black macula and at subapical black band.

Head. Eyes extremely large, laterally protruding, strongly rounded; antennae very long, slender, antennal insertions nearly visible dorsally; anterior margin of clypeus



Figures 24–29. *Eretes australis*, larva. (24) Habitus, left lateral aspect. (25) Head, dorsal aspect. (26) Mandible, ventral aspect. (27–28) Maxilla: (27) dorsal aspect; (28) ventral aspect. (29) Labium, ventral aspect.

broadly V-shaped; anterior margin of labrum broadly excavated, excavation with relatively long setae extending over mandibles; anterior margin of labium densely beset with setae; apical labiopalpomere irregularly shaped, apically expanded, dorsally with large, elongate, oval sensory patch; lateral margin of labium with numerous setae; sensory processes of epipharynx very large, elongate oval and flattened (Fig. 1). *Thorax*. Prosternal process shallowly convex medially, apically elongate and sharply pointed, basally with numerous spinous setae; male protarsal palette with two large adhesive discs on basal tarsomere and very many small discs on tarsomeres 2–3; posterior dorsal surface of protarsomere 1 with two or more long, robust, sharp setae,

surfaces of protarsomeres 2–3 each with one or two similar setae; protibia and profemur relatively slender; profemur with ventral series of long natatory setae; mesotibia and femur each with ventral series of long natatory setae; mesotarsomeres 1–4 (both sexes), and protarsomeres 1–4 (females only), each with two long, slender spinous setae ventrally; mesotarsomeres covered with small, aciculate, adpressed setae; male without ventral adhesive setae on mesotarsomere; metafemur with posterior series of short, natatory setae; metatibia posteriorly with ventral series of stout, spinous setae; apically with oblique series of long, bifid setae; at apex with margin of bifid setae and few simple setae; metatarsomeres with anterior and posterior surfaces covered with aciculate, adpressed setae (e.g., Fig. 2); anterior metatarsal claw shorter than posterior; both relatively straight; pronotum laterally evenly but only slightly curved, posterolateral angles acutely rounded; lateral margin narrowly beaded; elytron moderately punctate; apicolateral margin of elytron with even series of short, stout setae; apex of elytron distinctly pointed (Figs. 15–23); metendosternite (Figs. 4, 5) with anterior arms elongate, relatively straight, distance between arms (anterior emargination) very narrow; lateral arm elongate, extending slightly posteriorly; ventral arm apically acute, distinctly visible in dorsal aspect; in lateral aspect metendosternite with apex bent ventrally; metathoracic wing (Fig. 6) lightly pigmented; oblongum cell broad, posterior margin relatively long, medially margin strongly curved; subcubital binding patch present but weakly pigmented. *Abdomen*. Sternum three with numerous, short, spinous setae, otherwise not strongly modified.

Male genitalia (Figs. 7–10). Lateral lobes relatively narrow, elongate, with one or more large spinous setae directed ventrally at apex and a large field of smaller spinous setae along lateral margin in apical half; lateral lobes very broadly connected ventrally by strong membrane, membrane with ventral field of anteriorly-directed spines apico-medially. Median lobe long, slender, with lightly sclerotized, lateral, longitudinal processes extending from about half the length of the median lobe to about level of apex; apex of median lobe variably expanded and modified; ventral sclerite reduced, integrated into ventral membrane of lateral lobes.

Female genitalia (Figs. 11–14). Gonocoxosternite elongate-triangular, medial margin relatively straight or slightly convex, anterolateral lobe prominent, bilobed; gonocoxae fused, together apically medially emarginate, apex of each gonocoxa with ventral pencil of posteriorly directed, elongate setae; laterotergite slender, curved, apex extending posterad of apices of gonocoxae; rami elongate, lightly sclerotized extending to or nearly to apices of gonocoxae. Vagina moderately long, moderately broad; spermathecal duct broad; spermatheca moderately long, curved, of even diameter throughout; fertilization duct slender, indistinct.

Sexual dimorphism. Females with short, mediolateral sulcus on elytron (except in *E. australis*); sulcus absent in males. Males with protarsomeres 1 to 3 broadly expanded into a bowl-shaped, circular disc with many ventral, adhesive setae, each shaped like a round saucer at the apex of a stem, with many small setae and with two basal setae with much larger apical sucker discs; female protarsomeres not expanded and without

adhesive setae. Females with elongate apicolateral spines ventrally on both sides of pro- and mesotarsomeres 1 to 4; males without setae on protarsomeres and spines on mesotarsomeres 1–4 shorter. Many females with lateral pronotal margin slightly sinuate or straight; males with lateral pronotal margin more evenly curved. Overall, females average slightly (about 1 mm), but significantly longer than males (*p*-value from *t*-test = 0.023).

Distribution. The single genus is approximately circumtropical with species from Australia, throughout southeast Asia from Indonesia to Japan and from numerous oceanic islands, through India and the Middle East, throughout Africa including Madagascar and several Atlantic islands, through southern Europe and in the New World from Peru north through the Caribbean to Florida and through Mexico to the southeastern and central United States.

Comments. One character, the sensory processes of the epipharynx, used in the diagnosis of this group, requires some explanation since it is not commonly used in Dytiscidae. The epipharynx in dytiscines is mainly membranous with numerous sensory structures. The largest structures are the paired processes termed the 'Gaumenzapfen' by Hochreuther (1923). Although occurring in various shapes and sizes among the dytiscines examined (including members of *Dytiscus* Linnaeus, *Hyderodes* Sharp, *Notaticus* Zimmermann, *Hydaticus* s. str. Leach, *H.* (*Guignotites*) Brinck, *Acilius* Leach, *Graphoderus* Dejean and *Thermonectus* Dejean), they are in no examined taxa shaped as in *Eretes* where they are very large, elongate and flattened and bear a large number of sensory pores (Fig. 1).

Larvae of *Eretes* were described by Mayet (1887), Meinert (1901) and Bertrand (1949) and figured and keyed by Bertrand (1972). Both larvae and pupae were superficially described by Nowrojee (1912). Therefore, larvae are not described here in detail though important phylogenetic features are illustrated (Figs. 24–29, see Discussion), and select measurements of the larva of *E. australis* are provided (Table 3).

Eretes Laporte, 1833

Eunectes Erichson, 1832 (not Wagler, 1830, Reptilia: preoccupied, replaced by *Eretes* Laporte, 1833; type species *Dytiscus sticticus* Linnaeus, 1767, by monotypy); Aubé, 1838; Gemminger and Harold, 1868; Nilsson et al., 1989.

Nogrus Dejean, 1833 (type species *Dytiscus griseus* Fabricius, 1781, by subsequent designation of Hope (1838)); Nilsson et al., 1989.

Eretes Laporte, 1833 (type species *Dytiscus griseus* Fabricius, 1781, by original designation); Crotch 1873; Sharp, 1882; Leng, 1920; Guignot, 1961; Zimmermann, 1919, 1920; Nilsson et al., 1989.

Key to the species of *Eretes*

1 Median lobe of male genitalia in lateral aspect with dorsal margin straight to rounded apex (Fig. 9A, E); apices of gonocoxae broadly rounded, apical emargination of gonocoxae of female genitalia relatively narrow (Fig. 13); Middle East, throughout Africa and New World from Peru to southwestern United States and Caribbean . . . . . *E. sticticus*

– Median lobe of male genitalia in lateral aspect with dorsal margin distinctly sinuate due to apical expansion (Figs. 7A, E, 8A, E, 10A, E); apices of gonocoxae of female genitalia more narrowly rounded, apical emargination of gonocoxae broader and deeper (Figs. 11, 12, 14) 2

2 Female elytron without mediolateral longitudinal sulcus; lateral lobe of male genitalia apically very slender, with a single large apical spine and relatively few smaller spines (Fig. 7C, D); median lobe as in Fig. 7A, B, E; Australia . . . . . *E. australis*

– Female elytron with mediolateral longitudinal sulcus; lateral lobe of male genitalia apically broader, generally with three or more large apical spines and relatively more smaller spines (Figs. 8C, D, 10C, D); median lobe as in Figs. 8A, B, E, 10A, B, E 3

3 Apical expansion of median lobe of male genitalia large (Fig. 8A, B, E); gonocoxae of female genitalia with apices narrowly rounded, apicomedial emargination deep and broad, laterotergites long relative to gonocoxae, extending well beyond apices of gonocoxae (Fig. 12); transverse black band on elytron generally well-developed (Fig. 19); southern Europe, throughout Africa, southern Asia to the Russian Far East, Japan and the Philippines south to extreme northern Australia . . . . . *E. griseus*

– Apical expansion of median lobe of male genitalia smaller (Fig. 10A, B, E); gonocoxae of female genitalia with apices more broadly rounded, apicomedial emargination not as broad or deep, laterotergites not as long relative to gonocoxae, extending to just beyond apices of gonocoxae (Fig. 14); transverse black band on elytron generally not well-developed (Figs. 22, 23); central North America . . . . . *E. explicitus*

Eretes australis (Erichson, 1842) (Figs. 7, 11, 15, 16, 24–29)

Eunectes australis Erichson, 1842 [Type locality—Australia (here restricted)]; Gemminger and Harold, 1868.
Eunectes punctipennis MacLeay, 1871 [Type locality—Gayndah, Queensland, Australia].
Eretes australis, Sharp, 1882; van den Branden, 1885; Zimmermann, 1919, 1920; Watts, 1978.
Eretes punctipennis, van den Branden, 1885; Zimmermann, 1920; Guignot, 1961.

Diagnosis. Male genitalia distinctive, median lobe in lateral aspect with dorsal margin sinuate, apex with expanded region, dorsally slightly pointed, apex rounded (Fig. 7A, E), lateral lobe apically relatively narrow, generally with a single large, spinous seta and a long, narrow lateral series of short, spinous setae (Fig. 7C, D). Female genitalia distinctive, with apices of gonocoxae moderately narrowly rounded, medial emargination relatively broad (Fig. 11). Body relatively small and narrow with transverse black band on elytra generally entirely absent, with only a few larger black macula on some specimens (Fig. 15, 16). Female without lateral elytral sulcus. Measurements in Tables 1–3.

Variation. This species is perhaps the least variable species in color in the genus. Nearly all specimens have the dorsal maculae limited mainly to the punctures and expanded only at the lateral spot and in spots along the three longitudinal series, but

Table 1. Measurements and ratios for *Eretes* species. All measurements in millimeters. Provided are sample range and sample mean ± sample standard deviation. Abbreviations; *n* = sample size, TL = total length, GW = greatest width, PW = greatest pronotal width, HW = narrowest width of head between eyes, EW = greatest width of head across eyes, PL = medial length of pronotum, EL = length of elytron from base of pronotum to apex of elytron.

		TL	GW	PW	HW	EW	PL
australis	all *n* = 20	12.29–17.31	6.24–8.59	4.58–6.21	3.15–3.87	1.44–1.92	1.65–2.12
		14.74 ± 1.41	7.53 ± 0.69	5.33 ± 0.46	3.52 ± 0.21	1.67 ± 0.14	1.87 ± 0.13
	♂ *n* = 10	12.29–14.96	6.24–7.79	4.58–5.40	3.15–3.71	1.44–1.72	1.65–2.12
		13.80 ± 0.96	7.07 ± 0.50	5.04 ± 0.32	3.44 ± 0.20	1.58 ± 0.10	1.89 ± 0.15
	♀ *n* = 10	13.48–17.31	7.03–8.59	5.04–6.21	3.30–3.87	1.53–1.92	1.65–1.98
		15.69 ± 1.15	7.99 ± 0.53	5.61 ± 0.39	3.59 ± 0.19	1.75 ± 0.13	1.85 ± 0.11
griseus	all *n* = 20	10.87–16.25	6.11–9.15	4.38–6.20	3.09–4.02	1.44–1.99	1.51–2.17
		14.19 ± 1.40	7.87 ± 0.77	5.55 ± 0.52	3.64 ± 0.28	1.72 ± 0.14	1.84 ± 0.17
	♂ *n* = 10	10.87–15.62	6.11–8.86	4.38–6.20	3.15–3.97	1.44–1.99	1.66–2.17
		14.17 ± 1.50	7.76 ± 0.84	5.59 ± 0.64	3.68 ± 0.30	1.71 ± 0.15	1.90 ± 0.17
	♀ *n* = 10	11.95–16.25	6.83–9.15	4.80–6.12	3.09–4.02	1.56–1.98	1.51–1.94
		14.21 ± 1.37	7.98 ± 0.73	5.52 ± 0.42	3.60 ± 0.28	1.73 ± 0.14	1.78 ± 0.14
sticticus	all *n* = 20	13.06–18.87	6.96–9.85	4.98–6.86	3.38–4.25	1.53–2.31	1.74–3.78
		15.81 ± 1.62	8.35 ± 0.83	5.9 ± 0.49	3.79 ± 0.26	1.88 ± 0.20	2.17 ± 0.43
	♂ *n* = 10	13.55–17.10	6.96–8.67	5.07–6.31	3.39–4.02	1.53–2.31	1.87–2.40
		15.37 ± 1.11	8.11 ± 0.58	5.90 ± 0.43	3.78 ± 0.24	1.91 ± 0.21	2.11 ± 0.16
	♀ *n* = 10	13.06–18.87	7.12–9.85	4.98–6.86	3.38–4.25	1.56–2.13	1.74–3.78
		16.25 ± 1.96	8.60 ± 1.00	5.90 ± 0.58	3.80 ± 0.30	1.85 ± 0.20	2.23 ± 0.60
explicitus	all *n* = 20	14.74–18.06	7.55–14.50	5.46–6.53	3.63–4.31	1.69–2.06	1.77–2.35
		16.34 ± 0.98	8.83 ± 1.45	6.02 ± 0.30	4.01 ± 0.18	1.88 ± 0.11	2.11 ± 0.15
	♂ *n* = 10	14.74–17.71	7.55–14.50	5.46–6.31	3.79–4.17	1.69–2.00	2.02–2.28
		16.13 ± 0.80	8.90 ± 2.01	6.01 ± 0.27	4.02 ± 0.14	1.85 ± 0.10	2.15 ± 0.09
	♀ *n* = 10	14.96–18.06	7.76–9.44	5.49–6.53	3.63–4.31	1.69–2.06	1.77–2.35
		16.54 ± 1.14	8.76 ± 0.62	6.03 ± 0.34	4.00 ± 0.21	1.91 ± 0.11	2.06 ± 0.19

Table 2. Measurements and ratios for *Eretes* species. All measurements in millimeters. Provided are sample range and sample mean ± sample standard deviation. Abbreviations in caption for Table 1.

		EL	TL/GW	PL/PW	EW/HW	PW/GW	EL/TL
australis	all $n = 20$	9.54–13.66	1.87–2.09	0.31–0.42	0.44–0.52	0.67–0.76	0.76–0.82
		11.61 ± 1.24	1.96 ± 0.05	0.35 ± 0.03	0.47 ± 0.02	0.71 ± 0.02	0.79 ± 0.02
	♂ $n = 10$	9.54–11.42	1.87–2.04	0.34–0.42	0.44–0.48	0.67–0.74	0.76–0.80
		10.68 ± 0.74	1.95 ± 0.05	0.37 ± 0.02	0.46 ± 0.01	0.71 ± 0.02	0.77 ± 0.01
	♀ $n = 10$	10.94–13.66	1.89–2.09	0.31–0.35	0.46–0.52	0.68–0.76	0.79–0.82
		12.53 ± 0.88	1.96 ± 0.06	0.33 ± 0.01	0.49 ± 0.02	0.70 ± 0.02	0.80 ± 0.01
griseus	all $n = 20$	8.09–13.40	1.66–1.93	0.30–0.40	0.43–0.53	0.67–0.76	0.74–0.82
		11.32 ± 1.24	1.80 ± 0.06	0.33 ± 0.02	0.47 ± 0.03	0.71 ± 0.02	0.8 ± 0.02
	♂ $n = 10$	8.09–12.42	1.68–1.93	0.30–0.40	0.43–0.53	0.70–0.76	0.74–0.81
		11.21 ± 1.38	1.83 ± 0.07	0.34 ± 0.03	0.46 ± 0.03	0.72 ± 0.02	0.79 ± 0.02
	♀ $n = 10$	9.52–13.40	1.66–1.85	0.30–0.34	0.46–0.53	0.67–0.71	0.79–0.82
		11.44 ± 1.15	1.78 ± 0.05	0.32 ± 0.01	0.48 ± 0.02	0.69 ± 0.01	0.8 ± 0.01
sticticus	all $n = 20$	10.31–15.23	1.72–2.00	0.30–0.60	0.40–0.66	0.65–0.74	0.76–0.84
		12.57 ± 1.42	1.89 ± 0.06	0.37 ± 0.06	0.50 ± 0.05	0.71 ± 0.03	0.79 ± 0.02
	♂ $n = 10$	10.31–13.35	1.72–2.00	0.31–0.39	0.40–0.66	0.69–0.74	0.76–0.82
		12.11 ± 0.94	1.90 ± 0.08	0.36 ± 0.03	0.51 ± 0.07	0.73 ± 0.02	0.79 ± 0.01
	♀ $n = 10$	10.38–15.23	1.81–1.97	0.30–0.60	0.45–0.52	0.65–0.73	0.78–0.84
		13.04 ± 1.70	1.89 ± 0.05	0.38 ± 0.08	0.49 ± 0.02	0.69 ± 0.02	0.8 ± 0.02
explicitus	all $n = 20$	11.56–14.72	1.13–2.15	0.31–0.39	0.43–0.51	0.41–0.76	0.76–0.82
		13.04 ± 0.81	1.88 ± 0.19	0.35 ± 0.02	0.47 ± 0.02	0.69 ± 0.07	0.8 ± 0.02
	♂ $n = 10$	11.56–13.47	1.13–2.15	0.32–0.39	0.43–0.49	0.41–0.76	0.76–0.81
		12.76 ± 0.57	1.87 ± 0.27	0.36 ± 0.02	0.46 ± 0.02	0.70 ± 0.10	0.79 ± 0.01
	♀ $n = 10$	11.94–14.72	1.78–1.99	0.31–0.38	0.45–0.51	0.65–0.72	0.77–0.82
		13.33 ± 0.94	1.89 ± 0.07	0.34 ± 0.02	0.48 ± 0.02	0.69 ± 0.02	0.81 ± 0.02

Table 3. Measurements and ratios for third instar larvae of *Eretes australis*. All measurements in millimeters. Provided are sample range and sample mean ± sample standard deviation. Abbreviations: HL = length of head from anterior margin of clypeus to posterior margin of head; HW = greatest width of head; FC = medial length of frontoclypeus from anterior margin of clypeus to base of ecdysial suture; A = total length of antenna (derived by adding A1; A2, etc.); A1, A2, etc. = total length of individual antennomeres; MP = total length of maxillary palpus (derived by adding MP1, MP2, etc.); MP1, MP2, etc. = total length of individual maxillary palpomeres; LP = total length of labial palpus (derived by adding LP1, LP2); LP1, LP2 = total length of each individual labial palpomere; MA = length of mandible; UG = total length of urogomphus. n = 7 for all measurements except maxillary palpomere, antenna and urogomphus each n = 6.

HL	2.27–2.63	2.40 ± 0.13	**A**	1.61–1.81	1.67 ± 0.07
HW	2.04–2.51	2.26 ± 0.18	**A1**	0.08–0.09	0.09 ± 0.01
HL/HW	0.99–1.13	1.07 ± 0.05	**A2**	0.61–0.73	0.66 ± 0.05
FCL	0.98–1.06	1.02 ± 0.03	**A3**	0.05–0.09	0.07 ± 0.01
ST	0.75–0.84	0.80 ± 0.03	**A4**	0.28–0.33	0.30 ± 0.02
MA	1.29–1.49	1.34 ± 0.09	**A5**	0.04–0.07	0.06 ± 0.01
MP	1.02–1.27	1.13 ± 0.10	**A6**	0.28–0.34	0.31 ± 0.02
MP1	0.11–0.13	0.12 ± 0.01	**A7**	0.16–0.21	0.18 ± 0.02
MP2	0.33–0.44	0.40 ± 0.04	**Al/A2**	0.11–0.15	0.14 ± 0.02
MP3	0.06–0.09	0.07 ± 0.01	**A3/A4**	0.19–0.31	0.23 ± 0.05
MP4	0.27–0.34	0.31 ± 0.03	**A5/A6**	0.13–0.22	0.19 ± 0.04
MP5	0.05–0.06	0.05 ± 0.01	**LP**	0.78–1.05	0.94 ± 0.09
MP6	0.14–0.23	0.18 ± 0.03	**LP1**	0.37–0.56	0.51 ± 0.07
MP1/MP2	0.25–0.32	0.29 ± 0.02	**LP2**	0.35–0.49	0.43 ± 0.05
MP3/MP4	0.20–0.27	0.23 ± 0.03	**UG**	1.26–1.54	1.42 ± 0.09
MP5/MP6	0.28–0.36	0.30 ± 0.03			

these are also small (Fig. 15). Very few specimens were examined that have a well-developed subapical black band (Fig. 16).

Distribution. This species is known only from Australia where it is very widespread, common and abundant (Fig. 30). It is allopatric with all other species, though it may be narrowly parapatric with *E. griseus*, which is rare in extreme northern Australia (Fig. 30).

Discussion. I examined the type of *E. australis* for this revision, but not the type of *E. punctipennis*. Watts (1978) established the synonymy of *E. punctipennis* based on his examination of the type of *E. puctipennis* (ANIC).

Type material examined

Eunectes australis: *lectotype* (designated here to clarify the assignment of this name to this species), ♂ in ZMHB labeled, '9736/ australis Er. Ter. Diemonsland Schayer [handwritten, blue label]/ Type [orange label]/ Hist.-Coll. (Coleoptera) Nr. 9738 Eunectes australis Er. Terra V. Diemensland Schayer Zool. Mus. Berlin [white label with black border]/ LECTOTYPE *Eunectes australis* Erichson, 1842 designated by K.B. Miller 2001;' *paralectotype*, 1 ♂ in ZMHB labeled, 'Hist.-Coll. (Coleoptera) Nr. 9738 Eunectes australis Er. Terra V. Diemensland Schayer Zool. Mus. Berlin [white label with black border]/ Type [orange label]/ PARALECTOTYPE *Eunectes australis* Erichson, 1842 designated by K.B. Miller 2001 [blue label];' *paralectotype*, 1 ♂ in ZMHB labeled same but also with '. . . Adelaide schomb./ 56911 . . .'

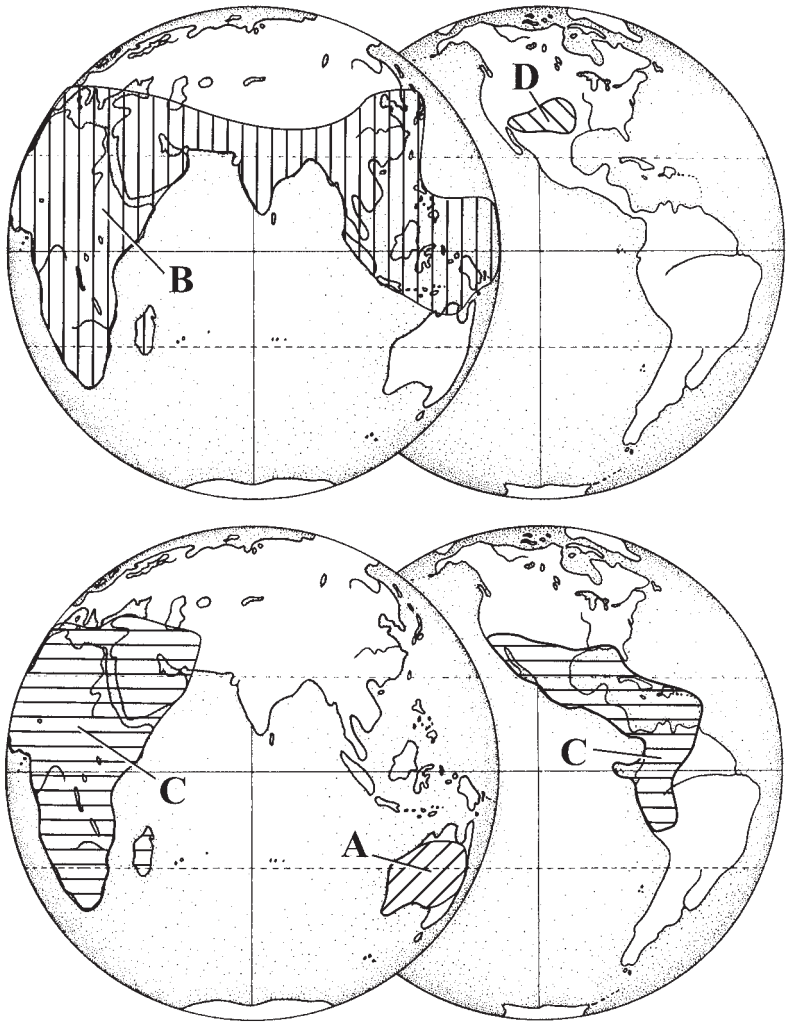


Figure 30. Maps indicating distributions of *Eretes* species. (A) *E. australis*. (B) *E. griseus*. (C) *E. sticticus*. (D) *E. explicitus*.

Eretes griseus (Fabricius, 1781), new status (Figs. 8, 12, 17–19)

Dytiscus griseus Fabricius, 1781 [Type locality—India].
Eunectes succinctus Klug, 1834 [Type locality—'Ambukohl' (probably Ámbikūl, Egypt)]; Gemminger and Harold, 1868; **new synonym.**
Eunectes plicipennis Motschulsky, 1845 [Type locality—Astrabad (Gorgon, Iran)]; Gemminger and Harold, 1868, **new synonym**.
Eunectes griseus, Gemminger and Harold, 1868.
Eretes succinctus, van den Branden, 1885; Zimmermann, 1920.
Eretes plicipennis, van den Branden, 1885; Zimmermann, 1920; Guignot, 1961.
Eretes griseus, van den Branden, 1885; Zimmermann, 1920.

Eretes sticticus griseus, Guignot, 1933, 1961.
Eretes sticticus succinctus, Zimmermann, 1919; Guignot, 1933, 1961.
Eretes sticticus moroderi Báguena Corella, 1935 [Type locality—Navarrés, Valencia, Spain (here restricted)], **new synonym**.
Eretes sticticus, Gschwendtner, 1954.

Diagnosis. Male genitalia distinctive; median lobe relatively broadly expanded apically, in lateral aspect with broadly rounded dorsal expansion at apex, ventral margin strongly sinuate (Fig. 8A, E). Female genitalia with gonocoxae together slightly expanded apically, apex of gonocoxa very narrowly rounded, appearing nearly pointed; medial apical emargination of gonocoxa relatively deep; laterotergites long, extending far beyond apices of gonocoxae (Fig. 12). Coloration variable, but typically with broad black subapical band on elytron more developed than in other species (Fig. 19). Measurements in Tables 1, 2.

Variation. The black subapical band on the elytron is variable in development, but is typically more strongly developed in specimens from Africa than in other parts of its range, such as in India and southeast Asia. This may be an example of character displacement since in Africa *E. griseus* co-occurs with *E. sticticus*, which generally lacks a strongly developed black band.

Distribution. This species occurs from Indonesia, the extreme northern tip of Australia (Darwin), and Guam to Japan and the Philippines to the Schezuan province of China and Vladivostok, Russia throughout southern Asia and Africa, including Madagascar, and north to southern Europe (Fig. 30). I have seen specimens from the following countries and regions; the Aldabra Atoll, Algeria, Australia, Botswana, Burma, China (Schezuan region), Egypt, Guam, Guinea Bissau, India, Japan, Java, Madagascar, Morocco, New Guinea, Nigeria, Pakistan, Philippines, Russia (Vladivostok, A. Nilsson, pers. comm.), Senegal, Sierra Leon, South Africa, Spain, Sudan, Sumatra, Taiwan, Thailand, Vietnam and Zaire.

Discussion. A single possible type specimen of *Eretes griseus* was examined from ZMUC labeled, 'Type [red label]/ Mus. Seh. et T. Lund [handwritten]/ Dytiscus griseus F. China Mus. T. Lund [handwritten].' However, the original description indicates that Fabricius had material from India, while this specimen's label indicates it is from China. Fabricius did not indicate the number of specimens available to him for the description, and it is possible the ZMUC specimen is a member of a syntype series. However, I am not confident about its identity as a member of the original type series or that other Fabricius specimens from India do not exist. Therefore, I have not designated the ZMUC specimen as a lectotype. I do not question the identity of *Eretes griseus*, however, since no other *Eretes* species appear to occur in either India (the type locality) or China.

The types of *E. succinctus* were examined and are members of this species. *Eretes griseus* has priority. Although I have not seen the type specimens of *E. plicipennis*, I strongly suspect that it refers to this species based on the description, the author's comparison of his specimens to *E. griseus* and the type locality, near the Caspian Sea in Iran where I would expect *E. griseus* to be more commonly collected than *E. sticticus*. The possibility remains that the species is not one of those treated here, but I

find this unlikely. I have also tentatively synonymized *E. s. moroderi* with this species based on the short diagnosis (Báguena Corella, 1935, 1942).

Gschwendtner (1954) circumscribed this species the same as I have, but he applied the name *E. sticticus* to it instead of *E. griseus* and applied the name *E. helvolus* to what I regard as *E. sticticus*. My examination of good images of the female holotype of *E. sticticus* has led me to apply this name to a different species (see below).

Type material examined

Eunectes succinctus: *Lectotype* (designated here to clarify the assignment of this name to this species), ♂ in ZMHB labeled, 'Type [orange label]/ Hist. Coll. (Coleoptera) Nr. 9733 Eunectes succinctus Klug Ambukohl. Ehrenberg Zool. Mus. Berlin [white label with black border]/ LECTOTYPE *Eunectes succinctus* Klug, designated by K.B. Miller, 2001 [red label];' *paralectotypes*, 1 ♂ 1 ♀ in ZMHB labeled same as lectotype but without red labels, one of these lacks head and prothorax; *paralectotype*, 1 ♀ labeled, '9733/ succinctus K* Amb. Ambuk. LXI.LXII [handwritten, green label with black line border]/ Hist. Coll. (Coleoptera) Nr. 9733 Eunectes succinctus Klug Ambukohl. Ehrenberg Zool. Mus. Berlin/ PARALECTOTYPE *Eunectes succinctus* Klug, designated by K.B. Miller, 2001 [blue label].'

Eretes sticticus (Linnaeus, 1767) (Figs. 1–6, 9, 13, 20, 21)

Dytiscus sticticus Linnaeus, 1767 [Type locality—Barbary, North Africa].
Eunectes helvolus Klug, 1834 [Type locality—'Ambukohl' (probably Ámbikūl, Egypt)]; Gemminger and Harold, 1868.
Eunectes punctatus Zoubkoff, 1837 [Type locality—Turkmenistan]; Gemminger and Harold, 1868.
Eunectes occidentalis Erichson, 1847 [Type locality—Peru]; Gemminger and Harold, 1868.
Eunectes conicollis Wollaston, 1861a [Type locality—St. Vincent, Cape Verde Islands]; Gemminger and Harold, 1868.
Eunectes subcoriaceus Wollaston, 1861b [Type locality—Madeira]; Gemminger and Harold, 1868.
Eunectes subdiaphanus Wollaston, 1861b [Type locality—Grand Canary Island]; Gemminger and Harold, 1868.
Eunectes sticticus, Gemminger and Harold, 1868; Wollaston, 1861a.
Eretes helvolus, Wollaston, 1871; van den Branden, 1885; Zimmermann, 1920; Gschwendtner, 1954.
Eretes occidentalis, van den Branden, 1885; Zimmermann, 1920; Gschwendtner, 1954; Guignot, 1961; Larson et al., 2000.
Eretes sticticus, Crotch, 1873; Zimmermann, 1919, 1920; Leng, 1920; Young, 1954; Guignot, 1961; Santiago-Fragoso, 1992.
Eretes conicollis, van den Branden, 1885; Zimmermann, 1920; Guignot, 1961.
Eretes punctatus, van den Branden, 1885; Zimmermann, 1920; Guignot, 1961.
Eretes subcoriaceus, van den Branden, 1885; Zimmermann, 1920; Guignot, 1961.
Eretes subdiaphanus, van den Branden, 1885; Zimmermann, 1920; Guignot, 1961.
Eretes sticticus helvolus, Zimmermann, 1919; Guignot, 1961.
Eretes stictica, Blackwelder, 1944.
Eretes occindentalis, Vazirani, 1977, incorrect subsequent spelling.

Diagnosis. Male genitalia distinctive, median lobe in lateral aspect with dorsal and ventral margins nearly parallel and straight to rounded apex (Fig. 9A, E), lateral lobe moderately broad apically with several large spinous setae and a large region of smaller spinous setae (Fig. 9B, C). Female genitalia also distinctive, apices of gonocoxae broad and apically broadly rounded, medial emargination of gonocoxae relatively narrow; gonocoxae with lateral margins divergent posteriorly (Fig. 13). Size generally larger than other species except *E. explicitus* (Tables 1, 2), usually with transverse elytral black band present but fragmented and indistinct (Figs. 20, 21). Measurements in Tables 1, 2.

Variation. This species is variable in the extent of dorsal maculations. The black maculae on the head and pronotum are variable in extent. Frequently the black macula on the pronotum is absent or vague. The subapical black band is generally irregular and weakly developed, but may be narrow and distinct to virtually absent (Figs. 20, 21).

Distribution. This species has a particularly unusual distribution for a dytiscid. It occurs in the Old World from the Middle East throughout Africa north to Cyprus, including the Cape Verde and Canary Islands, and in the New World from Peru and the Galapagos Islands to the Virgin Islands north to California, Arizona and Texas, USA (Fig. 30). I have seen specimens from the following countries and regions: Algeria, Botswana, Canary Islands, Cyprus, Ecuador (including the Galapagos Islands), Egypt, Iran, Kenya, Madagascar, Mexico (Sonora, Hidalgo, Baja California, Aguascalientes, Chihuahua, Coahuila and Sinaloa), Namibia, Peru, Puerto Rico, Zimbabwe, Saudi Arabia, South Africa, Sudan, United Arab Emirates, the USA (Arizona, California and Texas), Venezuela and the Virgin Islands (St. Croix and St. John).

Discussion. The unusual distribution of this species would seem to suggest that at least two species may actually be involved, one in the Old World and another in the New World. However, I cannot find any consistent differences between these two groups of populations in male or female genitalia or other characters. The male and female genitalia are both very distinctive and remarkably consistent among all specimens examined throughout all portions of its range. The presence of the species on numerous islands indicates the great vagility of the species, and it is certainly reasonable to hypothesize the conspecifity of the populations. Gschwendtner (1954), interestingly, came to a similar conclusion about the circumscription of this species and also considered it as having both New and Old World populations. However, he applied the name *E. helvolus* to this species reserving the name *E. sticticus* for what I regard as *E. griseus*. I regard *E. occidentalis*, the only *Eretes* name based on New World populations, to be a junior synonym based on examination of the female lectotype and its distribution. It should be noted that Larson et al. (2000) regard all New World populations as belonging to the species, *E. occidentalis*, based on an extensive morphometric analysis, a hypothesis which appears to be unsupported by known discrete character differences as interpreted during this study.

Although I did not examine the holotype of *E. sticticus*, I did examine high quality photographs of the specimen generously provided by S. Hine (BMNH). It is a female labeled, '12/ sticticus [handwritten].' The specimen lacks a transverse black band on the elytra and is relatively elongate. This, combined with its collection locality, 'Barbary, N. Africa,' (an area where this species appears to be commonly found) led me to conclude that the name refers to the species described above. Since it is the oldest name for this species, it is the valid name.

E. conicollis, *E. subcoriaceus* and *E. subdiaphanus* were each described from several specimens (Wollaston, 1861a; 1861b), but I have seen only a single specimen of each syntype series (BMNH) and have designated them as lectotypes.

Type material examined
Eunectes punctatus: *lectotype* (designated here to clarify the assignment of this name to this species), ♀ in ZMUH labeled, '♀ [handwritten]/ Karelin. [handwritten]/ Turcomannia. [handwritten]/ Eunectes punctatus Zoubk. SYNTYPE [red label]/ LECTOTYPE *Eunectes punctatus* Zoubkoff, 1837 designated by K.B. Miller, 2001;' *paralectotype*, 1 ♀ in ZMHB labeled same as lectotype. *Eunectes helvolus*: *lectotype* (designated here to clarify the assignment of this name to this species), ♂ in ZMHB labeled, 'helvolus [handwritten] Type [orange label]/ Hist.-Coll. 9732 Aegypt., Ehrenb. [handwritten] Zool. Mus. Berlin [white label with black border]/ LECTOTYPE *Eunectes helvolus* Klug, 1834 designated by K.B. Miller, 2001 [red label];' *paralectotypes*, 2 ♀ in ZMHB labeled same as lectotype but with '. . . / PARALECTOTYPUS/ PARALECTOTYPE *Eunectes helvolus* Klug, 1834 designated by K.B. Miller, 2001 [blue label];' 1 ♂ in ZMHB labeled same as lectotype but with '. . . / helvolus Kl.* Aegypt. XLII Ambuk. Ehrbg. [green label with black border]/ PARALECTOTYPE *Eunectes helvolus* Klug, 1834 designated by K.B. Miller, 2001/ [blue label].' *Eunectes occidentalis*: *lectotype* (designated here to clarify the assignment of this name to this species), ♂ in ZMHB labeled, '9735/ occidentalis Er. Peru V. Tschudi [handwritten, green label]/ Type [orange label]/ Hist. Coll. (Coleoptera) Nr. 9735 Eunectes occindentalis [sic] Er. Peru. V. Tshudi Zool. Mus. Berlin [white label with black line border / LECTOTYPE *Eunectes occidentalis* Erichson, 1847 designated by K.B. Miller, 2001/ [red label].' *Eunectes conicollis*: *lectotype* (designated here to clarify the assignment of this name to this species), ♂ in BMNH labeled, 'Co-type [round disc with yellow border]/ Cape Verde [handwritten, oval label]/ 67.56/ Eunectes conicollis. W [handwritten]/ LECTOTYPE *Eunectes conicollis* Wollaston, 1861 designated by K.B. Miller, 2001 [red label].' *Eunectes subcoriaceus*: *lectotype* (designated here to clarify the assignment of this name to this species), ♀ in BMNH labeled, 'Type [round disc with red border]/ 220. [round disc]/ subcoriaceus, Woll. [handwritten]/ LECTOTYPE *Eunectes subcoriaceus* Wollaston, 1861 designated by K.B. Miller, 2001 [red label].' *Eunectes subdiaphanus*: *lectotype* (designated here to clarify the assignment of this name to this species), ♀ in BMNH labeled, '[small, black square]/ Type [round disc with red border]/ Eunectes subdiaphanous type Woll. [handwritten]/ LECTOTYPE *Eunectes subdiaphanus* Wollaston, 1861 designated by K.B. Miller, 2001 [red label].'

Eretes explicitus, sp. nov. (Figs. 10, 14, 22, 23)

Diagnosis. Male genitalia distinctive, median lobe in lateral aspect with dorsal margin sinuate, apex distinctly expanded and curved dorsally (Fig. 10A, E), lateral lobe relatively broad apically, with numerous, large spinous setae and large region of smaller spinous setae (Fig. 10C, D). Female genitalia also distinctive, apices of gonocoxae acutely rounded, medial emargination narrow and deep (Fig. 14). Large species with transverse black elytral band reduced on most specimens (Figs. 22, 23). Measurements in Tables 1, 2.

Variation. This species is only moderately variable in the extent of dorsal maculae with most specimens bearing a fairly well-developed subapical black band, but with it ranging from distinctly present to nearly absent (Figs. 22, 23).

Discussion. Remarkably, given the large number of names in this genus, this species from central North America has remained undescribed. Although externally virtually identical to *E. sticticus*, the male and female genitalia are distinctly and consistently different in shape. The two species are sympatric or parapatric in parts of northern Mexico and southwestern United States where they can be distinguished only by dissection at this time. Because of this, I have labeled as paratypes only those specimens in the USNM from which I examined genitalia.

Etymology. From the Latin *explicitus*, meaning 'disentangled' to signify the difficulty in sorting out the names associated with this genus.

Distribution. This species occurs in central and southwestern North America (Fig. 30). I have seen specimens from Sonora, Mexico and Kansas, Oklahoma, Texas and New Mexico, USA.

Material examined
Holotype, ♂ in USNM labeled, 'TEXAS, Balmorhea State Park VII-7-1963 P.J. Spangler/ HOLOTYPE *Eretes explicitus* Miller, 2001 [red label with double black line border].' *Paratypes*, 37 ♂, 9 ♀, in USNM, all paratypes have label '. . . PARATYPE *Eretes explicitus* Miller, 2001 [blue label]'; same as holotype (12 ♂, 2 ♀); MEXICO, Sonora, 20.0 mi E. Ures, 12.VIII.1969, B.S. Cheary & A. Hardy (1 ♂). USA, ARIZONA, Pearce, 14.VII.1919, A. Wetmore (1 ♂, 1 ♀); Pima Co., Arivaca, 9.VIII.1970, Lenczy (1 ♂, 1 ♀); KANSAS, McPherson, 29.VIII (3 ♂, 1 ♀); Morton Co., 3.VIII.1924, C.O. Bare (1 ♂); Riley Co., Popenoe, 23.VI (1 ♂); Seward Co., Liberal, 3 mi NE, 12.VIII.1958, J.R. Zimmermann (1 ♂, 1 ♀); NEW MEXICO, Luna (1 ♂); Roswell, VII.1963, Lenczy (1 ♂); Torrace Co., VII.1925, C.H. Martin (1 ♂); OKLAHOMA, Garfield Co., 1960, J.F. Reinert (1 ♂); TEXAS, 10 mi W. Kent, 8.VII.1963, P.J. Spangler (1 ♂); Big Bend NP, 8-9.X.1966 (1 ♂); Brewster, Big Bend NP nr Nugent Mt, 8-9.X.1966 (1 ♂, 1 ♀); Brownsville, 3.V.1904, H.S. Barber (1 ♂, 1 ♀); Cameron Co., Brownsville, 17.IV.1967 (1 ♂); Georgetown, 15.VI.1954, D. Lauck (1 ♂); Hubbard & Schwartz (1 ♂); Kerrville, H. Lacey (1 ♂); Lee Co. (1 ♂); New Braunfols, III.1902, G.M. Greene (1 ♂); Santa Ana Wildlife Ref. nr Alamo, 18.XI.1966, A. & M.E. Blanchard (1 ♂); Victoria, 27.XII.1910, J.D. Mitchell (1 ♂); Victoria, 7.III.1915, J.D. Mitchell (1 ♂, 1 ♀).

Extinct Taxa

Eretes antiquus (Oustalet, 1870)

Eunectes antiquus Oustalet, 1870 [Type locality—Corent].
Eretes antiquus, Guignot, 1931.

Discussion. This is the only eretine species described from a fossil. However, placement of this species in *Eretes* was strongly questioned by Guignot (1933). Based on Oustalet's (1870) illustration and description of the fossil, I agree with Guignot (1933) that the species may not even belong to Dytiscidae, much less *Eretes*. However, without examination of the specimens, I am hesitant to make any formal changes to the classification of the species as this time.

Other Names Associated with *Eretes*

Eretes ater Chatanay, 1911 [***nomen nudum***].
Discussion. This species was mentioned briefly by Chatanay (1911). He suggests it to be a variety of *Eretes sticticus* from central Africa. The name is a *nomen nudum* as it does not appear elsewhere in the literature with description or indication.

Eunectes erichsonii White, 1847 [***nomen nudum***].
Discussion. This name presents a curious nomenclatural puzzle. White (1847) erected this name as an apparent replacement for '*Eretes helvolus* Erichson *nec* Klug' in reference to Erichson's (1842) treatment of Dytiscidae in Tasmania. Of course, since the name was erected without a description, it could only be available by an adequate indication (Article 12.2 of the Zoological Code). However, the only reference to *E. helvolus* by Erichson is in a paragraph listing the species described in *Eunectes*. Thus

there is certainly no new concept of *E. helvolus* presented by Erichson that would satisfy a proper indication. The page in Erichson's work referenced by White is 134, the page on which Erichson describes *E. australis* and where Erichson makes no reference to *E. helvolus* at all. Possibly, White mistakenly thought Erichson named his Australian species '*E. helvolus*' rather than *E. australis*. It is also possible that White intended *E. erichsonii* as a replacement name (unneeded) for *E. australis*, though this seems even less likely and his reason for doing so is certainly not evident. Also, he is careful to cite the replaced name as '*nec* Klug' clearly indicating he intended to replace a homonym of one of Klug's names. In any case, I interpret White's name, *E. erichsonii*, as lacking a proper indication. Therefore, it is a *nomen nudum*.

Nogrus pallidus Dejean, 1833 [***nomen nudum***].
Discussion. This name probably refers to the species *E. griseus* given its attribution to specimens from Asia (Dejean, 1833; Gemminger & Harold, 1868). It is apparently an unpublished manuscript name first appearing in the Dejean (1833) catalog. The name was attributed by Dejean to Eschscholtz, but the name is a *nomen nudum* as it was not accompanied by a description or adequate indication.

Eretes sticticus a. *arevaloi* Báguena Corella, 1935 [**infrasubspecific and unavailable**].

Eretes sticticus a. *lutescens* Báguena Corella, 1935, 1942 [**infrasubspecific and unavailable**].

Discussion. The nomenclature of these names is confusing. *Eretes sticticus* a. *lutescens* is introduced in a key to the varieties of *Eretes* (Báguena Corella, 1935), though in a later paper it is also listed again as new (Báguena Corella, 1942). *Eretes sticticus moroderi* is introduced as a new name in his earlier paper (Báguena Corella, 1935). However, in the later paper (Báguena Corella, 1942) he lists a different name, *E. s.* a. *arevaloi*, though this name is based on exactly the same diagnosis and the same type localities (Navarrés and Millares). I think it is safe to conclude that the name *E. s. moroderi* was inadvertantly replaced by *E. s.* a. *arevaloi* in his second paper. Based on the short diagnoses presented by Báguena Corella (1935, 1942), I believe all these names to refer to the same species as *E. griseus*. As the two names, *E. s.* a. *lutescens* and *E. s.* a. *arevaloi* were introduced as 'aberrations' they are not available according to Article 54.6.2 of the Zoological Code.

Discussion

Previous cladistic analyes (Miller, 2000, 2001) indicate that *Eretes* is phylogenetically placed well within the Dytiscinae with Aciliini as its sister tribe. This is supported particularly by the form of the posterodorsal series of setae on the metafemur which are apically bifid and arranged in a strongly oblique row with the bases of the setae more-or-less contiguous (Fig. 3). Additional data from larval characters further support this relationship. Members of Aciliini and Eretini share the following putative larval synapomorphies: 1) similar ability to swim with body able to strongly and

quickly flex medially (Fig. 24); 2) ocelli modified, anterodorsal two distinctly enlarged, anteroventral ocellus directed anteriorly (Figs. 24, 25); 3) mandible with ventral margin of apical orifice serrate (Fig. 26); 4) cardo of maxilla broad and with medial and lateral rows of long setae; and 5) anteromedial margin of labium with a single, spinous process (possibly homologous with two processes present in Hydaticini and single, lobe-like glabrous process present in Cybistrini).

Unfortunately, although the genus has a number of strong synapomorphies, very few characters were discovered to group species within the genus. However, one character, the presence or absence of a lateral sulcus on the female elytron, suggests a sister group relationship between *E. australis*, which lacks the sulcus, and a group containing the other species, which possess it. Apart from this character, members of *E. sticticus* and *E. explicitus* are extremely similar to each other in non-discrete characters such as relatively large size and general similarity in shape, etc.

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