posterior edge trisinuate. Promesothoracic interlocking mechanism weakly developed. Prosternum in front of coxae longer than shortest diameter of a coxal cavity, slightly convex, without paired carinae; anteriorly truncate, without chin piece. Prosternal process complete, parallel-sided, slightly overlapping mesoventrite, apically acute. Procoxae projecting well below prosternum, without concealed lateral extensions. Trochantins broadly exposed and not fused to notum. Procoxal cavities transverse, very narrowly separated, externally broadly open, without narrow lateral extensions; internally open. Scutellar shield well developed, not abruptly elevated, posteriorly truncate. Elytra 2.6–2.9 times as long as combined width and 3.7-4.9 times as long as pronotum, without distinct puncture rows or reticulate sculpturing; apices conjointly rounded; epipleura very narrow, wider at base and apex. Mesoventrite separated by complete sutures from mesanepisterna, which are well separated from one another; anterior edge on same plane as metaventrite, without paired procoxal rests; mesoventral cavity small and shallow. Mesocoxae projecting. Trochantins exposed. Mesocoxal cavities contiguous, weakly defined, open laterally (partly closed by mesepimeron, and mesanepisternum). Metaventrite slightly convex, with long discrimen and no transverse suture; exposed portion of metanepisternum moderately elongate. Metacoxae contiguous, extending laterally to meet elytra; plates narrow but more or less complete. Metendosternite with lateral arms short, laminae absent, anterior process moderately long and anterior tendons approximate. Hind wing elongate with very short apical field containing a single anterior oblique sclerite; radial cell elongate with inner posterobasal angle more or less right; cross-vein r3 well developed and very slightly oblique; basal portion of RP very long; medial field with five free veins; MP₃₊₄ with basal cross-vein and spur, joined by CuA₁ before forking; wedge cell well developed, apically truncate; anal lobe well developed but without distinct embayment. Legs long and simple; tibial spurs paired on all legs; tarsi 5-5-5, tarsomeres simple, without pubescent pads or membranous lamellae; pretarsal claws simple, without setae near base. Abdomen with seven ventrites (sternites III-IX), the first three of which are connate. Ventrite 1 not much longer than 2, without intercoxal process. Spiracles located in pleural membrane, those on segment VIII functional. Anterior edge of sternite VIII without median strut. Anterior edge of sternite IX without spiculum gastrale. Tergite IX deeply emarginated. Tergite X well developed and free. Aedeagus trilobate, symmetrical; parameres individually articulated, with slight outward hooks; penis with paired anterior struts. [Lawrence et al. 1999]

Phylogeny and Taxonomy. The family Plastoceridae was proposed by Crowson (1972) for *P. angulosus* (Germar) and was placed in Cantharoidea. Lawrence and Newton (1995) transferred the family

to Elateroidea along with the other "cantharoid" families. The *Plastocerus* concept used by Crowson (1972) and Lawrence & Newton (1995) is based upon the original concept of Schaum (1852), and does not include the North American species once placed by LeConte (1861) in *Plastocerus*, which now belong to *Octinodes* (Elateridae: Cebrioninae). Also excluded from the family are the diverse genera placed in here by Schwarz (1907) and currently included in Eucnemidae: Phyllocerinae (*Phyllocerus* Serville and *Cephalodendron* Latreille) or in various subfamilies of Elateridae (*Aphricus* LeConte, *Aplastus* LeConte, *Diplophoenicus* Candèze, *Dodecacius* Schwarz, *Enisonyx* Horn, *Euplastius* Schwarz and *Euthysanius* LeConte).

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4.9. Family Drilidae Blanchard, 1845

Ladislav Bocak, Marc A. Branham and Robin Kundrata

Distribution. Drilidae is a small elateroid family with approximately 100 species classified in only six genera: *Drilus* Olivier (25 spp.), *Euanoma* Reitter (8 spp.), *Malacogaster* Bassi (10 spp.), *Paradrilus* Kiesenwetter (1 sp.), *Pseudeuanoma* Pic (3 spp.), and

Selasia Laporte (about 50 spp.) (Kundrata & Bocak 2007). Most genera and species occur in the Mediterranean region, usually with restricted ranges corresponding to Pleistocene refugia in the Iberian Peninsula (Paradrilus), or Greece, Turkey, and the Causassus (Euanoma and Pseudeuanoma). The genera Drilus and Malacogaster are widespread in the Mediterranean, but only two species of Drilus occur north of the Alps. Selasia is known from the Afrotropical Region, Arab Peninsula, and Suqutra. [Bahillo de la Puebla & López Colón 2005; Kundrata & Bocak 2007; Kleine 1942; Wittmer 1944.]

Biology and Ecology. Drilidae occur in various habitats with populations of terrestrial mollusks upon which their larvae feed (Cros 1930; Gittenberger 1999; Orstan 1999; Mesher & Welter-Schultes 2001; Symondson 2004). There are no records of feeding by adult males (Crowson 1972). Drilidae are most common in lowland or lower mountain forest habitats in central Europe and from costal marshes to high altitude habitats in the Mediterranean. Adult males of Mediterranean species are diurnal, but they show maximum activity in the evening hours before sunset when there is high humidity and lower temperature. They frequent the vegetation of herbal and lower shrub strata, where they can be collected by sweeping from late March in low elevations in southern Europe and till the end of July in the mountains. Although they are capable of slow, reluctant flight, their vagility is generally very low and species ranges appear very restricted. All known females of the genera Drilus, Malacogaster and Selasia are wingless, with a larviform morphology of the thorax and abdomen and they can be found along with larvae in empty mollusk shells or foraging on the soil surface. The larvae of *Drilus* and Malacogaster are thought to feed on one individual land snail during each instar. Each instar is spent within the snail shell, feeding at first, then using the shell for shelter and ultimately pupating within the shell. In early instars, multiple larvae can be found within a single snail shell (Balduf 1935). The larval biology of the genera Paradrilus, Euanoma, and Pseudeuanoma is unknown, but similar life history is supposed also in these groups (Bahillo de la Puebla & López Colón 2005; Kundrata & Bocak 2007). Drilidae are mostly known only from males and due to their rareness they are poorly represented even in major European collections. The last record of the monotypic genus Paradrilus was at the end of the 19th century and the species may be extinct. The Afrotropical genus Selasia occurs commonly in forest and shrub habitats and their males are often attracted to light (Bourgeois 1882).

Morphology. Adult Males (Figs. 4.9.1–2). Moderately sclerotized beetles. Body form elongate, dorsoventrally flattened, parallel-sided to slightly widened posteriorly (Fig. 4.9.1 A). Length 2.4–10.8 mm. Coloration either dark brown to black (*Pseudeuanoma*, *Paradrilus*, most species of *Drilus*,

some *Selasia*) or light brown to yellow (most species of *Selasia*), seldom with bright red body parts (*Malacogaster*, some *Euanoma*). Vestiture sparse, often long, moderately erect. Pronotum and elytra sometimes shiny, with fine to rough, dense sculpture.

Head hypognathous, small, only slightly retracted into prothorax. Transverse, width including eyes almost as wide as pronotum at frontal margin; prolonged anteriorly in some genera. Antennal insertions widely separated, anterolaterally oriented and barely visible from above; subantennal grooves shallow. Eyes (Fig. 4.9.1 B) lateral, hemispherically prominent, their frontal interocular distance 1.15–2.60 times eye diameter. Antennae stout, 11segmented, reaching one third of elytral length, narrowed to apex; filliform in Euanoma, Pseudeuanoma and Paradrilus, strongly serrate to flabellate in Drilus and Malacogaster, flabellate with very long lamellae in Selasia; scapus robust, pear-shaped, slightly asymmetrical; length of antennomeres 2–4 variable, antennomere 2 shorter than 3 in Drilus, Malacogaster and Selasia, subequal in Euanoma, Pseudeuanoma and Paradrilus (Figs. 4.9.1 F-J); following antennomeres gradually shortened, except terminal one; all antennomeres with moderately dense, erect pubescence. Frontoclypeal suture absent; anterior edge of frontoclypeus concave. Labrum membranous anteriorly, with long setae at apex. Mandibles long, slender, considerably curved, incisor margin simple or with teeth in middle (Fig. 4.9.1 L). Maxilla with fused galea and lacinia (Fig. 4.9.1 K). Maxillary palpi small, 4-segmented; basal palpomere very short, transverse; palpomere 2 3.5 times longer than palpomere 1, widened to apex; palpomere 3 short, transverse; palpomere 4 almost as long as palpomere 2, parallelsided to gradually narrowed to apex, with obliquely truncate, membranous apex. Labium transverse, without ligula. Labial palpi small, 3-segmented; apical palpomere similar in shape to apical maxillary palpomere (Fig. 4.9.1 E).

Pronotum flat, 1.22-1.45 times wider than length at midline, widest in anterior third, seldom widest at base (Fig. 4.9.1 C); disc surface sometimes shiny, margins always finely to coarsely punctured; punctures at margins dense, gradually more sparse medially or roughly punctured across entire surface; shallow longitudinal depression along midline present in some species; entire disc with sparse, erected, long setae. Posterior angles sharp, prominent to rectangular; posterior edge bisinuate or widely rounded; lateral edges sinuate or convex; anterior edge straight or slightly concave. Prosternum long (e. g., Pseudeuanoma, Euanoma) or more transverse (Drilus, Selasia), without apparent prosternal process (Fig. 4.9.1 D). Scutellum small, simply rounded at apex. Mesoventrite with frontal margin straight (Euanoma), shallowly emarginate (Drilus) or deeply emarginate (Pseudeuanoma). Elytra flattened, almost parallel-sided to slightly widened posteriorly, widest in apical third, 2.20-2.90 times longer than width at humeri; shiny, with sparse to dense, fine, erected pubescence; longitudinal costae

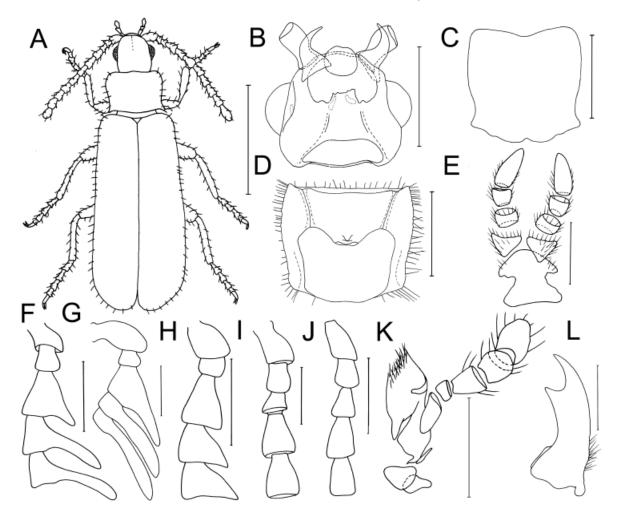


Fig. 4.9.1. A, Euanoma starcki Reitter, general appearance, line = 1 mm; B, Pseudeuanoma sp., head ventrally, line = 0.5 mm; C, Pseudeuanoma ionica Pic, pronotum, line = 0.5 mm; D, Pseudeuanoma sp., prothorax, ventrally, line = 0.5 mm; E, Drilus concolor Olivier, labium, line = 0.25 mm; F, Drilus flavescens Olivier, basal antennomeres, line = 0.5 mm; G, Selasia pulchra Pascoe, basal antennomeres, line = 0.5 mm; H, Malacogaster sp., basal antennomeres, line = 0.5 mm; I, Pseudeuanoma sp., basal antennomeres, line = 0.25 mm; J, Paradrilus opacus Kiesenwetter, basal antennomeres, line = 0.25 mm; K, Drilus concolor Olivier, maxilla, line = 0.5 mm; L, Drilus concolor Olivier, mandible, line = 0.25 mm.

absent, at most with very weak, irregular, longitudinal rows of punctures. Hind wings (Fig. 4.9.2 A) fully developed in all males (never brachypterous or apterous); apical field very short, bearing oned or two anterior oblique sclerites and another posterior one; radial cell large with inner posterobasal angle slightly acute; cross-vein r3 very long and oblique; medial field with two or three free veins and no wedge cell; anal lobe well developed, without embayment. Legs slender, slightly flattened; coxae well separated; trochanters robust; femur attached apically; tibia without apical spurs; tarsi with five slender tarsomeres. Claws simple.

Abdomen with seven ventrites. Terminal male segments as in Fig. 4.9.2 H. Aedeagus of trilobate type, with fine sickle-shaped phallobase, regularly with processes at base; parameres fused basally; phallus strong, usually longer than parameres, widest at base, sometimes considerably curved (Figs. 4.9.2 B–G); internal sac membranous or slightly sclerotized, rod-shaped.

Morphology, Adult Females (Fig. 4.9.3 A–D). Length 13–35 mm. Larviform, with elongate body (*Drilus*, *Malacogaster*) or robust (*Selasia*), slightly flattened dorsoventrally, parallel-sided (*Drilus*, Fig. 4.9.3 A) to considerably widened posteriorly (*Selasia*). Cuticle soft, weakly sclerotized (*Drilus*) or moderately sclerotized (*Selasia*). Vestiture usually dense, often long, erect. Coloration yellowish brown to dark brown.

Head small, prognathous, slightly transverse, half the width of the prothorax. Small compound eyes lateral, flat, their frontal distance about 3 times eye diameter in lateral view. Antennal sockets inconspicuous, widely separated. Antennae robust, very short, as long as width of head, filliform, 10-segmented. Scapus robust, pear-shaped, slightly asymmetrical; antennomere 2 shorter; apical antennomere very small and narrow in *Drilus* (Fig. 4.9.3 B). Mandibles long, slender, distinctly curved towards apex; incisor margin with teeth. Both palpi small, with basal palpomeres very slender,

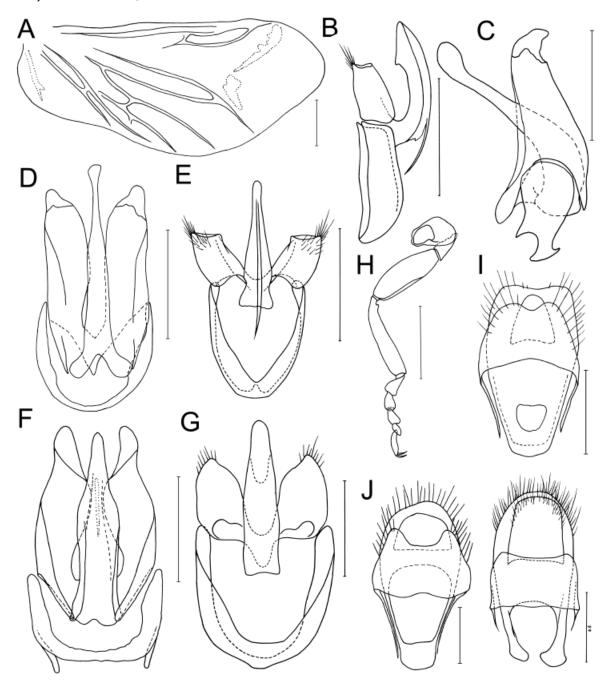


Fig. 4.9.2. A, *Pseudeuanoma* sp., wing, line = 2 mm; B, *Selasia* sp., male genitalia, lateral view, line = 0.5 mm; C, D, *Euanoma curvata* Kundrata & Bocak, male genitalia, lateral and ventral view, line = 0.25 mm; E, *Selasia* sp., male genitalia, ventral view, line = 0.5 mm; F, *Euanoma svihlai* Kundrata & Bocak, male genitalia, ventral view, line = 0.25 mm; G, *Drilus concolor* Olivier, male genitalia, ventral view, line = 0.25 mm; H, *Pseudeuanoma sp.*, hind leg, line = 0.5 mm; I, *Euanoma starcki* Reitter, apical abdominal segments, line = 0.25 mm; J, *Pseudeuanoma reitteri* Pic, apical abdominal segments, line = 0.5 mm.

subapical palpomere transverse, and apical palpomere pointed.

Thoracic segments larviform, slightly narrower than those of abdomen. Elytra and wings absent. Legs similar to those of males, but shorter, with widely separated coxae; claws paired (Fig. 4.9.3 C).

Abdomen with nine visible segments. Widest in posterior third; apical segment IX much narrower and smaller. Ovipositor with coxites plate-like, fused with paraproctal baculi (Figs. 4.9.3 D). Styli

small, articulate, connected to coxites by extensive membrane. Vagina simple, sac-like, membranous, with unpaired extensive glands. [Kundrata & Bocak 2007; Cicero 1988; Wittmer 1989.]

Morphology, Larvae (internal characters only verified for *Drilus*; Beutel 1995) (Figs. 4.9.4 A–C). Larvae elongate, sometimes slightly twisted dorsally into a C-shape, slightly flattened. All but last instar with a conspicuous vestiture of long setae, especially on

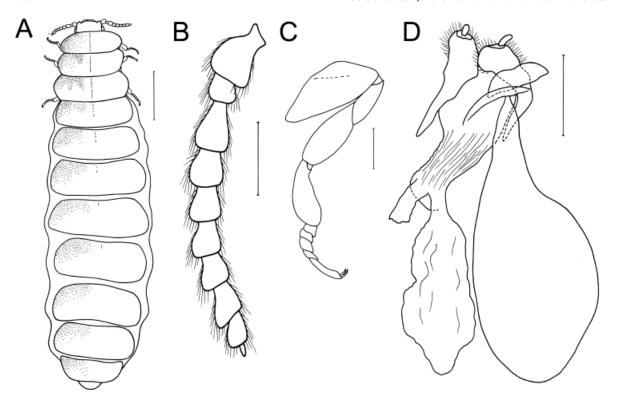


Fig. 4.9.3. A–D, *Drilus flavescens* Olivier, female, A, general appearance, line = 5 mm; B, antenna, line = 0.5 mm; C, hind leg, line = 0.5 mm; D, female genitalia, line = 1 mm.

dorsal surface of abdomen; with heavily sclerotized and pigmented tergites and slightly less heavily sclerotized ventrites (*Malacogaster and Drilus*) (Fig. 4.9.4 C).

Prognathous head sclerotized, short, partly retracted into prothorax. Epicranial sutures absent. Single stemma present on either side. Labrum fused to head capsule. Antennae 3-segmented; sensorium present on preapical segment; shorter than apical segment. Mandibles narrow and falcate, widely separated at base, slightly up-turned at tips; sucking channels present; mola and prostheca absent;. Ventral mouthparts form maxillolabial complex; exposed articulatory membrane absent. Cardo indistinct or absent; stipes subparallel, almost as long as head capsule; galea 1-segmented; maxillary palp, 4-segmented. Mentum (or postmentum) elongated; labial palp 2-segmented. Sclerotised gula present but strongly shortened. Tentorium vestigial. Antennal muscles with cranial origin; tentoriocardinal and tentoriostipital muscles almost vertical; lateral tentoriohypopharyngeal muscle absent. Dense, hairy preoral filter present; closed prepharyngeal tube elongated. Cerebrum located in the postoccipital region.

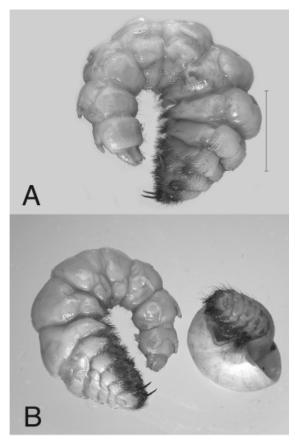
Prothorax subparallel, slightly widening posteriorly, nearly as long as meso- and metathorax combined. Legs 5-segmented, pretarsus with 2 spatulate setae. Mesothorax with biforous spiracles at ends of spiracular tubes.

Abdominal segments with well developed lateral tergal and pleural processes bearing long setae; lateral lobes more than twice as long as tergal lobes.

Spiracles I–VIII biforous, positioned between terga and pleura at the ends of spiracular tubes. Tergite IX with a pair of stout, fixed urogomphi with numerous well developed setae and a slender pointed apex. Segment X forming sucker-like pygopod. Luminous organs absent. [Böving & Craighead 1931; Lawrence 1991; Beutel 1995 (*Drilus*).]

Last larval instar strongly twisted dorsally into a C-shape, narrowing abruptly from posterior to anterior end. Setae restricted to dorsal surface of abdominal segments II-X (Malacogaster and Drilus): cuticle otherwise smooth, unsclerotized and light in color. Moderately sclerotized only in the dorsoposterior region of abdomen; abdominal segments bearing greatly reduced lateral tergal and pleural processes, both bearing short setae; lateral lobes more pronounced than tergal lobes (Fig. 4.9.4 A-B). Mandibles widely separated, greatly reduced. Legs reduced and shortened, less sclerotized than in earlier instars and lacking claws. Tergite IX bearing two paris of fixed, well sclerotized urogomphi; inner pair of setae twice as long as external pair. Segment X somewhat reduced. [Lawrence 1991; Balduf 1935; Crawshay 1903.]

Phylogeny and Taxonomy. Drilids were first described from western and southern Europe (Olivier 1790; Bassi 1834). Laporte (1836) described the Afrotropical genus *Selasia*, while other species were recognized from the eastern Mediterranean, northern Africa, and the Caucasus. Historically, only *Drilus*, *Malacogaster* and *Selasia* were originally assigned to Drilidae. The three remaining genera that are



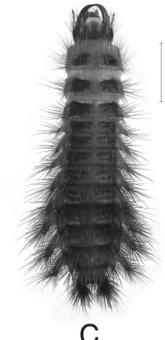


Fig. 4.9.4. A, *Malacogaster* sp. larvae, last instar larva, dorsolateral view, line = 5 mm; B, *Malacogaster* sp., last instar larva beside an earlier instar larva protruding from a broken snail shell, ventrolateral view; C, *Drilus* sp., larva, dorsal view, line = 5mm (A–C © M. Branham).

included within the modern concept of the family were originally assigned to Omalisidae (Bourgeois 1882; Kleine 1933). The French entomologist Maurice Pic described almost all Palaearctic species that

were added to Drilidae in the early 20th century (e. g., Pic 1901). Recently the Afrotropical genus Selasia was studied by Wittmer (1989) and Geisthardt (2003) and the genera Euanoma and Pseudeuanoma were investigated by Kundrata & Bocak (2007). The family has been historically classified near Lampyridae, Omalisidae and other families of soft bodied beetles in the superfamily Cantharoidea (sensu Crowson, 1955). In his revision of the classification of Cantharoidea, Crowson (1972), restricted Drilidae to the Palaearctic genera Drilus and Malacogaster, and the Afrotropical Selasia, and he provisionally transferred Pseudeuanoma from Omalisidae to Drilidae, while also mentioning the possibility that several less-diverse genera which were not available for his study may belong to Drilidae, such as for instance Euanoma, a genus close to Pseudeuanoma and Paradrilus, which was moved to Drilidae by Winkler (1925). The Oriental and east Palaearctic genera formerly classified in Drilidae (Olivier 1910; Wittmer 1944) were transferred to Lampyridae, Rhagophthalmidae, Omethidae, and Lycidae (Crowson 1972). The above listed genera were considered to compose Drilidae by Lawrence & Newton (1995). The monophyly of Drilidae in the present sense is weakly supported, without a single synapomorphy defining the family that is present in all genera (Kundrata & Bocak 2007). The position of Drilidae remains contentious. Beutel (1995) hypothesized their placement with Omalisidae, Lycidae and Lampyridae, while Branham & Wenzel (2003) hypothesized Drilidae to be a sister-group of all cantharoid families in their analysis. Molecular data (Bocakova et al. 2007) indicate a close relationship between Omalisidae, Drilidae and Elateridae. Consequently, Drilidae are suggested to be only distantly related to the remaining soft-bodied elateroid families such as Lycidae, Lampyridae and Cantharidae.

Acknowledgements

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4.10. Family Omalisidae Lacordaire, 1857

Ladislav Bocak and Milada Bocakova

Distribution. Two genera are contained in Omalisidae: *Omalisus* Geoffroy (5 species) and *Thilmanus* Gemminger (2 species) and *Phaeopterus* Costa, 1857 (1 species). *Omalisus fontisbellaquei* Geoffroy is widely distributed (western, southeastern and central Europe) and all other species are known from a small number of specimens from localities in southern Europe. Note that the generic name *Omalisus* Geoffroy was conserved by Opinion 1754 (ICZN, 1994).

Biology and Ecology. Omalisidae live in forest or shrub habitats. Adult males can be collected by general sweeping. Larvae of *O. fontisbellaquei* prey on millipedes (*Glomeris* sp.). This species occurs in lower montane deciduous forests and is locally abundant. Males are capable of flight, but they usually sit motionless on leaves in the lowest forest stratum. Females are wingless (Bertkau 1891) and remain in the surface soil and few specimens have been collected. Larval luminosity was reported incorrectly by Bertkau (1891) for *O. fontisbellaquei* (see also Beutel 1995) and refuted by Burakowski