

# CALICOVATELLUS PETRODYTES, A NEW GENUS AND SPECIES OF PRIMITIVE VATELLINE DIVING BEETLE (COLEOPTERA: DYTISCIDAE: HYDROPORINAE: VATELLINI) FROM THE MIOCENE BARSTOW FORMATION, SOUTHERN CALIFORNIA, USA

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RELATIVELY FEW fossil dytiscids have been described. This is unfortunate since fossils can provide useful phylogenetic and evolutionary information including unique character combinations not present in extant taxa and minimum ages for divergences. However, even when fossils are found, important characters are often not visible since they may be poorly preserved or obscured. The fossil insects present in calcareous nodules from the Miocene Barstow Formation of the Calico Mountains in Southern California are exceptionally well preserved (Palmer, 1957). The original organisms are replaced by silica or other minerals and when the nodules are dissolved in formic acid, the three-dimensional fossil can be retrieved from the resulting residue. These nodules have yielded a wide variety of fossils, including larvae of the dytiscid species *Schistomerus californense* Palmer, 1957 and numerous other terrestrial and fresh-water arthropods (Palmer, 1957). The purposes of this paper are to describe a new dytiscid genus and species from an exceptionally well-preserved specimen from the Barstow Formation and to present a hypothesis of the phylogenetic placement of the new taxon.

**Regional Geology.**—Beginning in the Miocene, Southern California was the site of extensive faulting and volcanic activity as the transform boundary between North American and Pacific Plates developed. The San Andreas Fault and its associated faults, including the Calico Fault (Glazner et al., 1994), mark this boundary. Right lateral movement along the San Andreas Fault formed the extensional basins of the Mojave region. These continental basins filled with fluvial and lacustrine sediments (Woodburne et al., 1990). The Barstow Formation fills an unnamed basin that extends from the Calico Mountains to the Gravel Mountains (Woodburne et al., 1990).

**The Barstow Formation and depositional environment.**—Hershey (1902) named the middle Miocene Barstow Formation (Fig. 1) after the town of Barstow, California. The formation consists of about 1,000 m of terrestrial sediments that were deposited in a basin formed after the Mojave block experienced a significant episode of extensional rifting and detachment faulting that caused uplift of the surrounding mountains (Woodburne et al., 1990). The discontinuous exposure covers approximately 75 square kilometers of the central Mojave Desert extending from the Gravel Hills in the west to the West Cronese Basin in the east and crops out in the Mud Hills, the Yermo Hills, the Alvord Mountains, and the Calico Mountains.

The Barstow Formation contains three members (Fig. 1): the Owl Conglomerate Member, and the unnamed middle and upper members. The Owl Conglomerate consists of granite and sandstone conglomerate, containing the Red division fauna of fossil mammals (Woodburne et al., 1990). The middle comprises coarse-grained fluvial and flood deposits from sources to the south and southwest. It contains fossil mammals of the Rak Division Fauna and Green Hills Fauna (Woodburne et al., 1990). The nodules containing the invertebrate fossils are known from the upper

member. The northern and eastern portions of the upper member contain lacustrine. The west and southwest portions contain alluvial fan deposits capped with fluvial deposits (Woodburne et al., 1990). The upper member also contains two fossil mammal assemblages: the Second Division Fauna and the Barstovian Fauna that characterizes the Barstovian Land Mammal Age (Lindsay, 1972).

The age of the Barstow Formation originally was determined using mammal biostratigraphy (Woodburne et al., 1990) and is supported by radiometric dating of the volcanic tuffs that separate its members (Fig. 1). The basal Red Tuff gives an oldest age for the Barstow Formation of 19 Ma, whereas the Lapilli Tuff at the top gives a minimum age of 13.3 Ma (Woodburne et al., 1990). The nodules are found in the upper layer which overlies the Sky-line Tuff that has been dated at 14.8 Ma (Woodburne et al., 1990).

**Collecting locality.**—Mule Canyon is located 3 km north of Yermo, California, on the southwestern border of the Calico Mountain range. During the middle Miocene a large shallow lake covered most of this area. Today, most of the lacustrine sediments are overlain by volcanic ash, the result of subduction along the North American and Pacific plate transform boundary. But, in Mule Canyon, the volcanic deposits have been eroded and the Barstow Formation sediments are exposed. The varved sediments in Mule Canyon are light-colored, grayish-white to greenish-tan shale with localized gypsum-rich beds hosting the insect-containing calcium carbonate nodules.

**The nodules.**—Although concretions containing fossils are not uncommon, nodules containing silicified insects are known only from the middle Miocene of Southern California.

The nodules are composed primarily of calcium carbonate and have a slight petroliferous odor. About half of the nodules contain petroleum (Pierce, 1964). They are disk or dome shaped, often with radial ridges on the outer surface, with diameters ranging from 0.5 to 5.0 cm.

The fossils are found only in the nodules and not in the surrounding sediments. They are three-dimensional and incredibly detailed. Insects decompose rapidly in the presence of oxygen (Elias, 1994), so the amount of detail preserved in the fossils indicates that the organisms were buried very quickly. After burial, the organic material degraded and was replaced with silica, leaving a very detailed cast of the original animal. Some fossils also contain celestite, gypsum, analcite, and calcite.

Several hypotheses have been proposed for the origin of the nodules. Degens et al. (1962) considered the nodules products of evaporation based on their measurements of oxygen isotopes, Pierce (1966) associated the nodules with boron deposits, and Jenkins (1986) called the nodules “stromatolitic growths”; however, S. Awramik, a stromatolite expert, disagrees (personal commun., 1996). Most recently, Park (1995) studied the geochemistry of Mule Canyon and determined that the nodules occur as the result of the concentration of carbonate ions from release of CO<sub>2</sub> and NH<sub>3</sub> during decomposition of organic matter under conditions

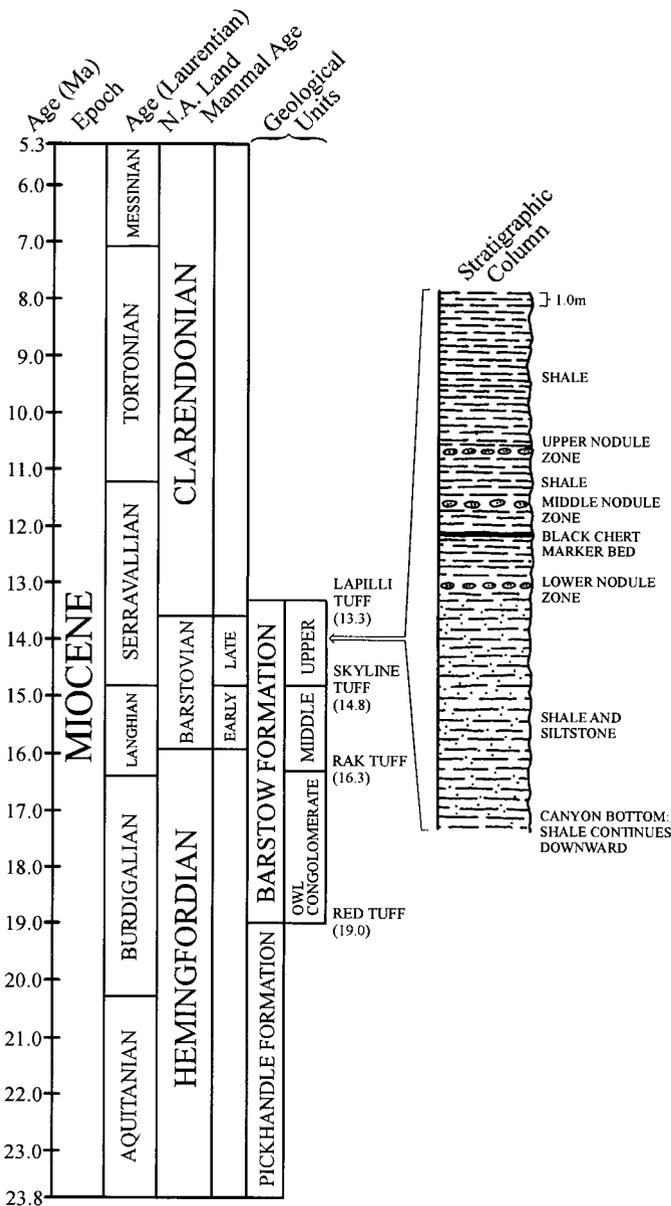


FIGURE 1—Stratigraphic table for the Barstow Formation with land mammal ages and dated tuffs used to determine the age of the formation. Included is a geologic column through Mule Canyon showing the three nodule-bearing zones.

of low energy Boron deposits. However, the origin of the nodules is still uncertain.

The nodules were first found to contain fossils in 1954 when Bassett of the USGS discovered an exposed dragonfly nymph on the surface of a weathered nodule (Palmer, 1957). He dissolved another nodule in formic acid in order to check for diatoms, and instead, he found fossilized insect larvae (Palmer, 1957). He brought these to the attention of Palmer, also of the USGS. Palmer dissolved several hundred nodules and discovered seventeen species of arthropods, including three that were not previously described (Palmer, 1957). Pierce and Rouse of the Los Angeles County Museum of Natural History subsequently dissolved over 30,000 nodules and described dozens of new species in a series of papers (Pierce, 1947, 1959, 1960a, 1960b, 1962, 1963, 1964, 1965, 1966; Pierce and Gibrón, 1962). Since then, several others

have also dissolved nodules and described their findings (Jenkins, 1986; McLaughlin, 1966).

MATERIAL AND METHODS

**Extraction of specimens.**—About 300 nodules were collected from Mule Canyon at a site approximately 50 m from the road (34°56'04"N 116°49'46"W; 823 m). To free the fossils from the calcium carbonate matrix, the nodules were dissolved in 10 percent formic acid. The recovered fossils are deposited in the paleontological collection of the Department of Geological Sciences, University of California, Santa Barbara.

**Condition of specimen.**—This description is based on a single, broken specimen. The head of the specimen is slightly extruded anteriorly and the prothorax is shifted slightly to the right. The appendages of the head and the legs are mostly missing. Also, the abdominal sterna and most of the metacoxae are missing. Fortunately, photographs of some of these structures were taken prior to their being damaged, and portions of the description are based on the photographs. Many important features important for diagnosing this taxon remain undamaged on the specimen. The specimen is remarkably intact for a fossil, nearly as perfect as many amber-preserved specimens, and perhaps better because the specimen is not embedded in resin and is, therefore, easily viewed from any angle. Structures, including surface sculpture, are very well-preserved. Within the body cavity even the wings and proventriculus can be discerned. Remarkably, even portions of the elytral color pattern are preserved. The specimen has been kept loose in a covered depression slide, but is now glued with water-soluble gum arabic and sugar to a paper point attached to an insect pin.

**Photographs and illustrations.**—Photographs are included here since these are the only information we have of certain structures which are now permanently damaged on the fragile specimen. Unfortunately, these photos are not well resolved. For this reason, line drawings are also included. Illustrations were made in part using a drawing tube on a Wild M3C dissecting microscope and in part from reference to the photographs of the more intact specimen. For this reason, illustrated structures of the abdominal sterna, metasternum, metacoxae, apex of the prosternal process and elytral apices, all of which are absent in the specimen, should be considered potentially less accurate than other portions of the illustrations.

**Measurements.**—Measurements were made using an ocular scale in a Wild M3C dissecting microscope at 16× magnification. Two measurements, total length and length of elytron along suture, were impossible to measure from the specimen because the apices of the elytra were broken. These two measurements were inferred by measuring photographs of the intact beetles and calculating ratios with known measurements. Therefore, they are likely to be less accurate. Also, the head of the specimen is extruded anteriorly, but the measurement of total length does not attempt to correct for this. Therefore, the total length is slightly inflated artificially.

SYSTEMATIC PALEONTOLOGY

- Order COLEOPTERA Linnaeus, 1758
- Family DYTISCIDAE Leach, 1817
- Subfamily HYDROPORINAE Erichson, 1837
- Tribe VATELLINI Sharp, 1882
- Genus CALICOVATELLUS new genus

**Type species.**—*Calicovateillus petrodytes* Miller and Lubkin new species, by present designation.

**Diagnosis.**—Diagnosible from all other genera of Dytiscidae by combination of: scutellum absent and prosternum and prosternal process strongly declivous, prosternal process not reaching metasternum and mesocoxal cavities contiguous (Fig. 2.2, 2.4),

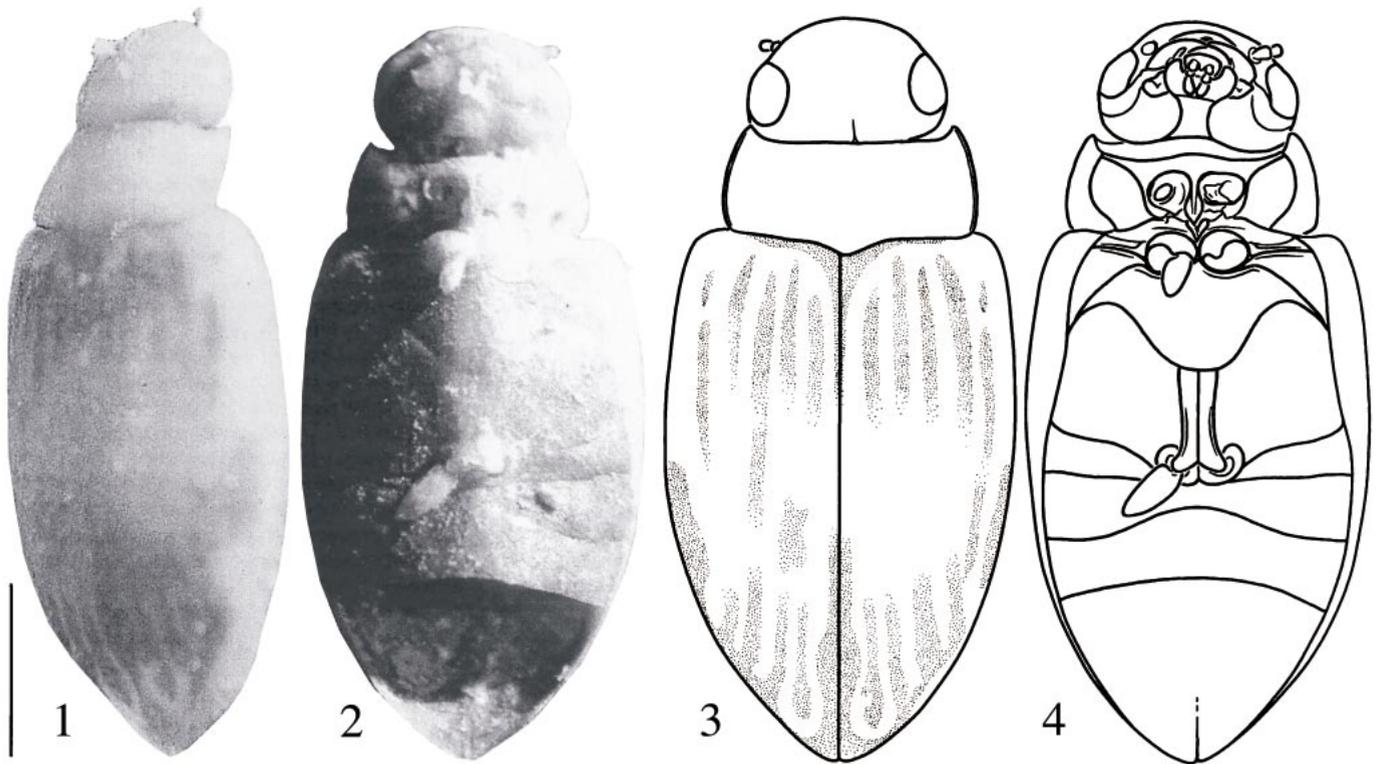


FIGURE 2—*Calicovatellus petrodytes* n. gen and sp., USNM 510565. 1, Right dorsolateral aspect; 2, ventral aspect; 3, dorsal aspect; 4, ventral aspect.

prothorax approximately quadrate and with posterior margin much narrower than anterior margins of elytra (Fig. 2.3), and metepisterna narrowly reaching mesocoxal cavities (Fig. 2.4).

**Etymology.**—This genus is named *Calicovatellus* from a combination of Calico, the name of a ghost town near the type locality and the mountain range where the Barstow Formation is exposed and the fossiliferous nodules were collected, and *vatellus*, the common root of the other genera in the tribe Vatellini.

**Occurrence.**—Lower nodule layer, Barstow Formation, Serravallian, Middle Miocene (Fig. 1). Mule Canyon, Calico Mountains, Mojave Desert, San Bernardino County, California, USA.

**Discussion.**—This adhephagan genus clearly belongs within Dytiscidae as evident from the greatly anteriorly enlarged metacoxae (Fig. 2.4). The concealed scutellum (Fig. 2.3) suggests that the genus belongs in either the Hydroporinae, Laccophilini or Aubehydrini. The strongly declivous prosternal process indicates it is a hydroporine. Within this subfamily, the genus is assigned to Vatellini as its general habitus resembles members of that group in having the prothorax relatively narrow and the posterior margin much narrower than the anterior margins of the elytra (Fig. 2.3). Also, the prosternal process does not attain the metasternum, the mesocoxae are contiguous, and the medial portion of the metacoxae are very narrow (Fig. 2.4), probable synapomorphies of the tribe. There are four described genera in the tribe, all extant: *Derovatellus* Sharp, *Macrovatellus* Sharp, *Mesovatellus* Trémouilles and *Vatellus* Aubé. These genera are the only members of the subfamily that have the metepisterna not reaching the mesocoxal cavities, a probable synapomorphy. All other Hydroporinae have metepisterna that reach the mesocoxal cavities, at least narrowly. *Calicovatellus* has the metepisterna reaching the mesocoxal cavities (Fig. 2.4), symplesiomorphic with other, non-vatelline hydroporines. We, therefore, hypothesize that *Calicovatellus* is the sister to a clade containing the remaining genera in the tribe based on this unique combination of character states.

CALICOVATELLUS PETRODYTES Miller and Lubkin new species  
Figure 2

**Diagnosis.**—Diagnosible by generic characters. Other potential species-level characters known to be useful in other dytiscids include characteristic shape of prothorax and elytra, relatively impunctate elytra, pronotum and head and characteristic, vittate pattern on elytra (Fig. 2.1, 2.3).

**Description.**—(Fig. 2.1–2.4). Total length = 4.43 mm, greatest width = 2.03 mm, length of elytron along suture = 3.11 mm, greatest width of pronotum = 1.38 mm, medial length of pronotum = 0.75 mm, greatest width of head = 1.11 mm, narrowest distance between eyes = 0.69 mm.

**Body elongate.**—Coloration of most of body apparently pale; elytra with six longitudinal, brown vitae, one along the suture, a shorter vita lateromedially and four long, discal vitae, the first of these ending posteriorly in a slightly expanded apex surrounded by pale color; also with diffuse, lateromedial elytral brown spot (Fig. 2.1, 2.3). Head moderately broad, dorsally impunctate. Pronotum narrow and subquadrate in dorsal aspect, distinctly narrower at posterior margin than anterior margin of elytra, greatest width moderately anterad of posterior margin (Fig. 2.3); posterolateral angles rounded (Fig. 2.3); lateral margins moderately rounded, more so posteriorly, margin narrowly beaded (Fig. 2.3); surface of pronotum apparently impunctate. Elytra elongate, lateral margins relatively parallel-sided (Fig. 2.3); apex of elytra rounded (Fig. 2.2–2.4); surface apparently impunctate; epipleuron impunctate, broad basally, narrowed near first abdominal sternite, medial margin broadly sinuate in anterior portion (Fig. 2.3). Prosternum narrow; prosternal process broad, apically acuminate, medially with small, longitudinal carina (Fig. 2.4); prosternum not reaching mesosternum, separated by mesocoxae (Fig. 2.4). Mesosternum moderately broad ventrally, narrowly visible laterad of prosternal

process (Fig. 2.4). Mesocoxae contiguous (Fig. 2.4). Metepisternum narrowly reaching mesocoxal cavities (Fig. 2.4). Mesosternum longitudinally moderately broad (Fig. 2.4); anterior mesosternal process slightly thickened. Metacoxa moderately anteriorly expanded (Fig. 2.4); lateral portion apparently impunctate; medially portion of metacoxa narrow, metacoxal lines subparallel, slightly more proximate posteromedially and slightly divergent anteriorly (Fig. 2.4); dorsal plane of metacoxal processes distinctly visible posterad of apical lobes of ventral plane (Fig. 2.4). Metatrochanter elongate oval, slightly narrowed apically (Fig. 2.4). Visible abdominal sternites 1–3 apparently impunctate; visible sternite 2 strongly narrowed medially because of anterior expansion of visible sternite 3.

*Etymology.*—From the Greek, *petro*, meaning “stone” and *dytes*, meaning “diver” since the specimen is a diving beetle found in a rock.

*Holotype.*—USNM 510565 (7-25-00).

*Occurrence.*—One specimen, stratigraphic range: Lower nodule layer, Barstow Formation, Serravallian, Middle Miocene (Fig. 1). Mule Canyon, Calico Mountains, Mojave Desert, San Bernardino County, California, USA.

*Discussion.*—A single genus and species of Dytiscidae has been described from these deposits, *Schistomerus californense* Palmer. This species was described from a large number of larval specimens representing all three instars and was placed in its own tribe, Schistomerini Palmer (Palmer, 1957). It is possible that these larvae are the same species as *C. petrodytes*. However, described larvae of other members of Vatellini, *Derovatellus* (Spangler, 1966) and *Macrovatellus* (Spangler, 1963), have very characteristic nasales with three long branches, and with the medial branch apically spatulate. Larvae of *S. californense* have a more typical hydrophiline type of nasale. Of course, given that *C. petrodytes* exhibits plesiomorphic characters for the tribe, it may be that its larvae are also plesiomorphic and lack these features. Nevertheless, because of absence of evidence for placement of *S. californense* in the tribe Vatellini, we do not regard this as the same species as *C. petrodytes*.

Although few things can be determined conclusively regarding the specific habitat requirements of this species, a few things can be inferred from the faunal and geological characteristics of the formation. Ninety-five percent of the fossil assemblage in the calcareous nodules belongs to only three larger groups (Lubkin, 1999). About 50 percent of the recovered fossils are anostracan crustaceans (brine shrimp), 35 percent of the fossils are pupae and larvae of ceratopogonid midges, and 10 percent are dytiscid beetle larvae (*S. californense*) (Lubkin, 1999). Other taxa, such as hydracarina, rhabdozoela, and ostracods are represented by only a few specimens (Pierce, 1964). Many of the fossils belong to taxa that can be good ecological indicators. Using the environmental requirements of these groups as limiting factors, it is possible to approximate some of the environmental conditions in Mule Canyon when the insects were buried and, thus, some of the possible habitat requirements of *C. petrodytes*. The presence of anostracans requires that the temperature in the lake be at least 4°C and probably higher than 6°C (Pennak, 1989). The upper temperature requirement for anostracans varies by species and may be as high as 30°C (Pennak, 1989). Anostracans require a minimum salinity of 3 percent NaCl (Ward, 1992). While anostracans can tolerate salinity up to the point of saturation, ceratopogonids cannot tolerate salinities above 14 percent NaCl (Ward, 1992). Neither anostracans nor hydracarina are known from water with pH below 6.8, and 7 to 7.5 is the normal range for anostracans (Moore, 1969). Chironomid midges and rhabdozoellan flat worms indicate that oxygen levels in the lake were low, and the presence of rhabdozoela, acarina, ceratopogonids and ostracods suggests a shallow lake with little wave action or wind mixing

(Pennak, 1989). Many of the fossil inhabitants of the lake belong to groups that possess adaptations for dealing with drought, so the lake may have dried up periodically. Therefore, the fauna and presence of evaporites such as borates and gypsum suggest that the lake was shallow, with still, warm, saline waters and that it was occasionally dry. This is certainly not inconsistent with the habitat requirements of many extant dytiscids in the southwestern United States and northern Mexico.

Young (1960) and Larson (1996) have noted the correlation between vittate, fasciate or mottled color patterns on some species of dytiscids and their occurrence in running water and/or water with mineral substrates such as frequently are found in desert environments. These patterns may be visually disruptive to predators as the beetles swim across the substrate (Larson, 1996; Young, 1960). There are a preponderance of hydrophiline genera with vittate elytra in western North America, such as members of *Stictotarsus* Zimmermann (1919) and *Oreodytes* Seidlitz (1887), that occur principally in habitats such as those mentioned above. The vittate elytra of *C. petrodytes* may have resulted from similar selective pressures as influenced these other groups, and it may have lived in water with a mineral substrate, a hypothesis supported by the geological evidence. Of course, this does not exclude the possibility that the vittate elytra in *C. petrodytes* may be a symplesiomorphy shared with a vittate ancestor and subsequently lost in the derived members of the tribe. It may be that the tribe Vatellini evolved from a desert inhabiting, vittate ancestor and that the clade that includes the extant genera of the tribe are secondarily lentic and non-vittate.

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