

Description of *Africanella* n. gen. (Gastropoda: Muricidae: Ocenebrinae) and review of some West African ocenebrine genera

Geerat J. VERMEIJ

Department of Geology and Center for Population Biology, University of California at Davis,
One Shields Avenue, Davis, CA 95616, U.S.A.

E-mail: vermeij@geology.ucdavis.edu

& Roland HOUART

Département des Invertébrés Récents, Institut royal des Sciences naturelles de Belgique.

Africanella n. gen. is described. It includes two West African species formerly assigned to *Ocenebra* Gray, 1847: *O. isaaci* Houart, 1984, and *O. coseli* Houart, 1989. *O. isaaci* is made the type of the new genus. The genus *Inermicosta* Jousseau, 1880, is reintroduced and a new generic combination is proposed.

Key words: Gastropoda, Prosobranchia, Muricidae, Ocenebrinae, *Inermicosta*, *Ocenebra*, West Africa.

INTRODUCTION

In his studies of West African and European muricid gastropods, Houart (1996, 1997, and in preparation) has uncovered a number of species whose generic assignment remains unsatisfactory. Several species previously assigned to *Ocenebra* Gray, 1847, and *Ocenebrina* Jousseau, 1880, do not closely match the type species of these genera, *Murex erinaceus* Linnaeus, 1758, and *M. aciculatus* Lamarck, 1822, respectively. Our purpose here is (1) to reintroduce the genus *Inermicosta* Jousseau, 1880, for one Recent tropical West African and several fossil species, (2) to erect the new genus *Africanella* for two Recent West African species and (3) to assign *Trophon gruveli* Dautzenberg, 1910 (a species previously assigned by Houart, 1997, to *Ocenebra*) to *Vaughtia* Houart, 1995.

Abbreviations: IRSNB= Institut royal des Sciences naturelles de Belgique, Brussels; MNHN= Muséum national d'Histoire naturelle, Paris.

SYSTEMATICS

Order Neogastropoda Thiele, 1929

Family Muricidae Rafinesque, 1815

Subfamily Ocenebrinae Cossmann, 1903

Remarks. — The muricid subfamily Ocenebrinae comprises a highly diverse assemblage of predatory gastropods whose classification above the species level has proved to be difficult. There is considerable intraspecific variation in the expression of axial and

spiral sculpture and of denticles on the inner (adaxial) side of the outer lip. Some potentially important features also vary ontogenetically. In many species, the siphonal canal becomes ventrally sealed at the time of formation of a varix, but it remains open during other growth stages. In other species, however, the formation of a varix leaves the siphonal canal open. Thus, although paedomorphosis could cause significant changes in shell form, some features are less affected by ontogeny and by changes in the rate of development.

Despite these problems, it is both possible and useful to discriminate phylogenetically meaningful groups within the *Ocenebrinae*. Such groups represent geographically circumscribed clades that can often be traced with fossil species to the Miocene or even the Oligocene. Progress in the supraspecific classification of this subfamily has been made through a combination of palaeontological, anatomical, and molecular studies (see Vokes, 1972; Kool, 1993; Houart, 1995, 1996, 1997; McLean, 1996; Bouchet & Houart, 1996; Vermeij & Houart, 1996; DeVries & Vermeij, 1997; Vermeij, 1993, 1995, 1998; Vermeij & Vokes, 1997; Marko & Vermeij, in review; Amano & Vermeij, 1998 a, b). In an effort to circumscribe supraspecific taxa, it is important to identify unique features or combinations of features. Vermeij (1998) provided a key to *ocenebrine* genera with a ventrally sealed canal, but did not treat closely related taxa in which the siphonal canal remains ventrally open in adulthood.

Although many eastern Atlantic fossil and Recent species have been assigned by previous authors to *Ocenebra* and *Ocenebrina*, few closely resemble the respective type species of these genera, *Ocenebra erinaceus* (Linnaeus, 1758) and *Ocenebrina aciculata* (Lamarck, 1822). Both genera have a relatively short, ventrally sealed siphonal canal. *Ocenebra* is characterized by a basally constricted last whorl, five to eight spiral cords and one to seven varices on the last whorl, and axial ribs that are angulated or lamellar. The outer lip lacks both a subsutural sinus and an anterior labral tooth, and the inner lip lacks an adapical parietal tooth. In *Ocenebrina*, the base of the last whorl is weakly constricted, and the last whorl bears a single terminal varix as well as low, rounded, axial ribs. Spiral sculpture on the last whorl consists of nine or more well marked cords, the most abapical of which occasionally ends in a short, blunt, labral tooth. An adapical sinus and parietal tooth are absent (see also Vermeij, 1998). The two genera differ in egg-capsule morphology (D'Asaro, 1991), as well as in size. Most species of *Ocenebra* exceed 30 mm in height, reaching a maximum of 65 mm, whereas most species of *Ocenebrina* are less than 20 mm high.

Genus *Inermicosta* Jousseume, 1880

Type species (by original designation): *Murex fasciatus* Sowerby, 1841 (= *Tritonalia inermicosta* Vokes, 1964).

Diagnosis. — *Ocenebrine* characterized by a multispiral protoconch consisting of about one and half smooth whorls and an additional whorl sculptured by two spiral keels; adult whorls with three varices per whorl, intervals between varices with intervarical node; spiral sculpture consisting of five upper and two very weak basal cords on last whorl; outer lip weakly erect, weakly denticulate on inner side, with shallow adapical sinus; small parietal tooth present at adapical end of inner lip; basally constricted; siphonal canal ventrally sealed.

Remarks. — In his catalogue of *Purpuridae* (= *Muricidae*), Jousseume (1880: 335) introduced the genus *Inermicosta* for *Murex fasciatus* Sowerby, 1841. The type species was

renamed *Tritonalia inermicosta* by Vokes (1964) in order to eliminate homonymy with *Murex fasciatus* Risso, 1826, and Gmelin, 1791. Jousseume (1882: 326) characterized *Inermicosta* as trivariolate, with an intervarical rib between adjacent varices, a small posterior canal, detached lips, and a sealed anterior canal. Besides the type species, Jousseume (1882) included *Murex festivus* Hinds, 1844, and *M. scalariformis* Nyst, 1861. The Recent northeastern Pacific *M. festivus* is now considered to be a somewhat aberrant species of *Pteropurpura* Jousseume, 1880, with abaperturally reflected varices (see Vokes, 1964; Vermeij & Vokes, 1997). Vokes (1971) assigned *M. scalariformis*, from the Miocene (Anversian = Burdigalian) of Belgium to *Calcitrapessa* Berry, 1959. That genus, based on *Murex leanus* Dall, 1890, from the Pleistocene and Recent of Baja California, has long, straight, adapically directed spines and a smooth shell essentially lacking spiral cords. Glibert (1952) considered *M. scalariformis* to be a variety of *M. delbosianus* Grateloup, 1833, from the Burdigalian of the Aquitaine Basin of southwestern France. Vokes (1971) assigned *M. delbosianus* to *Pteropurpura*. With its straight or recurved shoulder spines, *M. scalariformis* appears to be closely related to the Recent group of *Pteropurpura dearmata* (Odhner, 1922) from Angola and Namibia (see Houart, 1997).

In the years following Jousseume's publications, the name *Inermicosta* was applied to several European fossil species. Cossmann & Peyrot (1924) included *Murex granulifer* Grateloup, 1833 (Tortonian, southwestern France) and *M. dufrenoyi* Grateloup, 1840 (Burdigalian of southwestern France) in *Inermicosta* (as subgenus of *Murex* Linnaeus, 1758). They also mentioned *Murex exoletus* Bellardi, 1873 (Tortonian, Italy) as a member of this group. Glibert (1952) included *Murex vindobonensis ligeriana* Tournouer, 1875, in *Inermicosta*, which he treated as a section of *Tritonalia* Fleming, 1828 (= *Ocenebra* Gray, 1847). Vokes (1971) assigned *M. granulifer* to *Pterynotus*, whereas Baluk (1995) assigned it to *Purpura* (*Tritonalia*) (= *Ocenebra* Gray, 1847). The species may actually belong to *Pteryomarchia* Houart, 1995, a muricine genus today confined to the tropical Indo-West Pacific region. Baluk (1995) considered *Murex dufrenoyi* to be a *Purpura* (*Tritonalia*) (= *Ocenebra*), but Vermeij & Houart (1996) showed that its pattern of sculpture is that of *Jaton* Pusch, 1837. *Murex vindobonensis ligeriana* may be an *Ocenebra*.

Our review of some European fossil species indicates that several Oligocene and Miocene species may in fact belong to this genus. We discuss these briefly below.

The earliest possible species of *Inermicosta* are two Oligocene (Rupelian and Chattian) species, *Murex acuticostatus* Guembel, 1861, and *M. conspicuus* Braun in Sandberger, 1863, non Perry, 1811. Vokes (1971) considered these taxa synonymous. If this is correct, the single species would bear the name *Inermicosta acuticostata* (Guembel, 1861). Specimens under the name *Ocenebra conspicua* at IRSNB from Offenbach bear three varices on the last whorl, with a single intervarical node between adjacent varices. The outer lip bears five strong denticles on its adaxial side. The canal is open or sealed depending on the specimen. It is not clear from the material whether a subsutural sinus and parietal tooth are present, as they are in the type species of *Inermicosta*. Our assignment of this species to *Inermicosta* is therefore tentative.

Ocenebra cazeauxi Cossmann & Peyrot, 1924, from the Burdigalian and Helvetian (= Langhian) of southwestern France, was assigned by Vokes (1971) to *Ocenebrina*. According to Cossmann & Peyrot (1924), the later teleoconch whorls bear three varices, the outer lip has five denticles on its inner side, and the siphonal canal is short and sealed. We have not seen material of this species, and our assignment of it to *Inermicosta* is therefore tentative.

We are equally uncertain about our assignment of *Ocenebra colorata* Degrange-Touzin, 1894, to *Inermicosta*. This peculiar species from the Helvetian (= Langhian, middle

Miocene) of southwestern France, was assigned by Vokes (1971) to *Ocenebrina*. We have examined specimens from Orthez (le Paren), Pyrénées-Atlantique, at MNHN. The last whorl is weakly trivariolate, and the outer lip bears seven denticles on its inner side. There is a very weak parietal thickening at the adapical end of the inner lip. A unique feature of this species is a small, blunt, labral tooth, not previously noted by Cossmann & Peyrot (1924). This tooth forms as a slight ventral extension of the adaxial margin on the abapical portion of the outer lip. The abaxial margin of the outer lip remains unaffected. The mode of formation of this tooth is similar to that of the South American Miocene to Recent genus *Acanthina* Fischer von Waldheim, 1807 (see Vermeij, 1993). The siphonal canal is closed. *O. colorata* shares with *Inermicosta* the sealed canal, trivariolate condition, parietal tooth, and adaxial denticles. It differs from typical *Inermicosta* by the presence of the peculiarly formed labral tooth.

There may well be additional fossil species of *Inermicosta*. A thorough examination of material of the numerous European fossil species of *Ocenebra* and *Ocenebrina* will be needed to ascertain this point.

The only living species of the genus recognized thus far is the type species, *I. inermicosta*, a common shallow-water muricid found from Senegal to Angola.

The late Oligocene to late Pliocene genus *Pterylopsis* Vokes, 1972, from the eastern Atlantic resembles *Inermicosta* in having three varices on each of the adult whorls, but it differs by having a paucispiral instead of a multispiral protoconch, an open instead of a sealed siphonal canal, and, often, more than one intervarical node between adjacent varices, and by lacking denticles on the inner side of the outer lip, a parietal tooth and subsutural sinus. *Pterylopsis* also has fewer cords, and shows a tendency to form spines on the blade-like varices. *Chicocenebra* Bouchet & Houart, 1996, is another eastern Atlantic trivariolate genus, which differs from *Inermicosta* by having spiny varices, a long channelled shoulder spine on the varix, a high spire, an open siphonal canal, and a weakly unicarinate protoconch of 2.5 to 2.75 whorls. Moreover, *Chicocenebra* lacks a parietal tooth.

Genus *Africanella*, new genus

Type species: *Ocenebra isaaci* Houart, 1984 (figs. 1, 2, 12, 13).

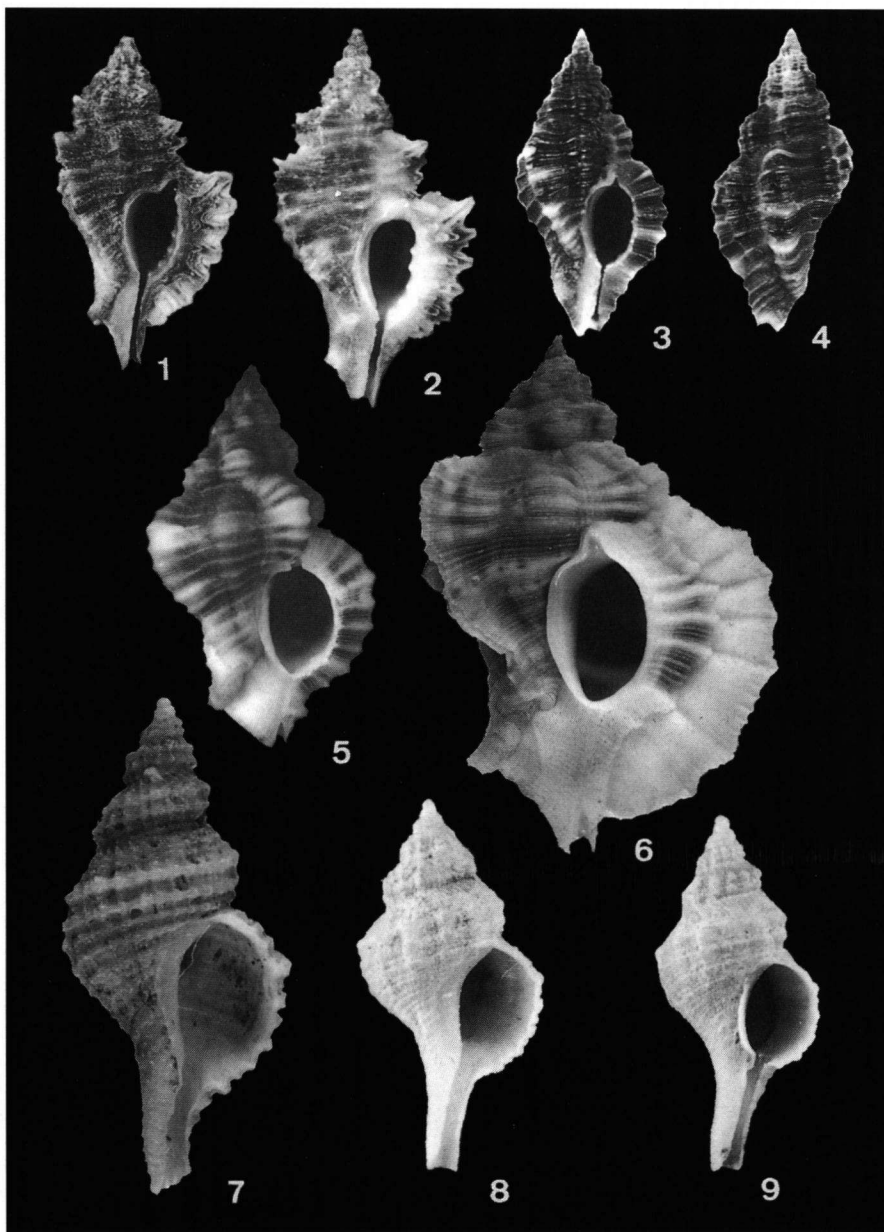
Other species. — *Ocenebra coseli* Houart, 1989 (figs. 3, 4, 11).

Description. — Shell small, maximum height 17 mm; fusiform, constricted at base; protoconch multispiral, unicarinate; spire high; last whorl or last two whorls with three varices, adjacent ones separated by a long intervarical rib; spiral sculpture on last whorl consisting of seven to ten fine, sharp cords separated by one to three finer threads; outer lip planar, crenulated at edge, with five to seven small denticles on adaxial side; posterior sinus or notch absent; inner lip narrow; smooth, with small parietal tooth at adapical end; siphonal canal short, ventrally open. Radula (Figures 12, 13): rachidian tooth with projecting short central cusp, two long lateral cusps with inner lateral denticle (basal projections), two long marginal cusps and marginal area with a two denticles; lateral tooth sickle-shaped with broad base. Operculum ovate, with basal nucleus.

Distribution. — Recent, tropical West Africa.

Etymology. — Combination of "Africa" and suffix meaning small.

Remarks. — Four tropical West African ocenebrines appear to be closely related to each other. All have trivariolate shells, and all have more or less similar, multispiral



Figs. 1-9. Shells of ocenebrine Muricidae. 1-2, *Africanella isaacsi* (Houart, 1984) from (1) Gabon, coll. R. Houart, 13 mm, and (2) Pointe Noire, Congo, MNHN, 17.3 mm; 3-4, *A. coseli* (Houart, 1989), Cape Esterias, Gabon, holotype MNHN, 9.3 mm; 5-6, *Inermicosta inermicosta* (Vokes, 1964) from (5) Gambia, coll. R. Houart, 33 mm, and (6) Luanda Bay, Angola, coll. R. Houart, 32 mm; 7, *Vaughitia babingtoni* (Sowerby, 1892), Mossel Bay, South Africa, coll. R. Houart, 15.3 mm; 8-9, *Vaughitia gruveli* (Dautzenberg, 1910), Mauritania, IRSNB IG 10591, (8) 11 mm (9) 10.3 mm.

protoconchs consisting of one to one and a half convex smooth whorls and an additional bicarinate whorl. This unusual type of protoconch perhaps reflects a secondarily derived planktotrophic larval life. The initial part of the protoconch closely resembles the entire, paucispiral protoconch of other ocenebrines, which have a nonplanktotrophic larval stage. *Inermicosta* differs from *Africanella* by having a sealed siphonal canal, by having the abapical keel of the protoconch almost concealed in the abapical suture, and by having a parietal tooth. *Chicocenebra* (fig. 10) differs from *Inermicosta* and *Africanella* by having four to five prominent spines on the varices, the shoulder spine being especially long and adapturally channeled, and by lacking a parietal tooth. Its siphonal canal is open, like that of *Africanella* but unlike that of *Inermicosta*. There are six to seven denticles on the adaxial side of the outer lip, and the last whorl is not constricted at the base. *Africanella* is distinguished by having the abapical protoconch carina strongly expressed, making the late part of the protoconch strongly bicarinate. The group is also characterized by an open siphonal canal and by the presence of a parietal tooth. The radula of the two species of *Africanella*, *A. isaacsi* and *A. cosei* (figs. 5, 6) differs from that of *Inermicosta inermicosta* by having a shorter, more projecting central cusp and longer marginal cusps. Whether all these differences deserve to be reflected in supraspecific taxonomy remains debatable. From similarities in shell and radular characters, we infer that the two species of *Africanella* form a cohesive group among the four West African species, but some authors might choose to recognize a single genus for all four species. The name *Inermicosta* would take precedence if such an interpretation were adopted. Additional work on the living species is needed to clarify the matter.

Differences with other genera are summarized under *Inermicosta*.

Genus *Vaughtia* Houart, 1995

Type species (by original designation): *Murex babingtoni* Sowerby, 1892.

Vaughtia gruweli (Dautzenberg, 1910) new combination, figs. 8, 9.

Remarks. — This species, which is distributed from the southern part of western Sahara to Mauritania, was originally described as a *Trophon*. Houart (1997, p. 551) tentatively assigned it to *Ocenebra*. The species has an open, long siphonal canal, a typically ocenebrine paucispiral rounded protoconch, and low axial ribs on the last teleoconch whorl. The radula is also typically ocenebrine (Houart, 1997). The smooth protoconch, broad last whorl, numerous axial ribs and spiral cords, long and open siphonal canal, and the radula of *Trophon gruweli* are all consistent with assignment of this species to *Vaughtia* (fig. 7), a genus otherwise known only from southern Africa.

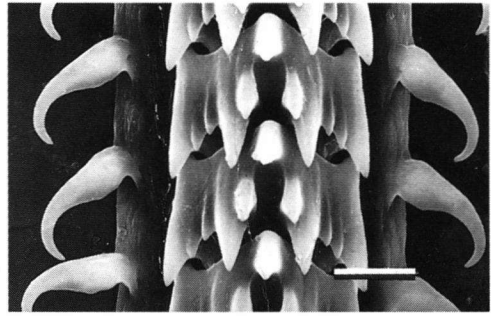
All other known species of *Vaughtia* are from South Africa. Besides the Recent species reviewed by Houart (1995), two extinct Pliocene species, *Ocenebra bonaccorsi* Carrington & Kensley, 1969, and *O. petrocyon* Kensley & Pether, 1986, also belong to *Vaughtia*. We have been unable thus far to assign any European fossil species to this genus.

ACKNOWLEDGMENTS

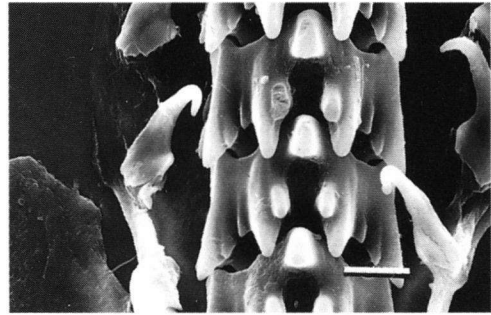
We thank J. Cooper for technical assistance, Greg Herbert for critically reviewing the manuscript, and the National Science Foundation for funding this research through grant NSF EAR-97-06749.



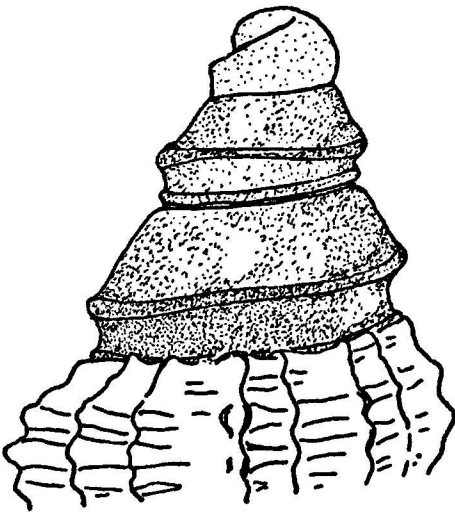
10



12



13



11

Figs. 10-13. Shells and radulae of ocenebrine Muricidae. 10, shell of *Chicocenebra gubbi* (Reeve, 1849), Gabon, coll. R. Houart, 49.1 mm; 11, protoconch of *Africanella isaacsi*, scale bar 0.5 mm; 12, radula of *Africanella coseli* (Houart, 1989), Gabon, scale bar 10 μ m; 13, radula of *Africanella isaacsi* (Houart, 1984), Angola, scale bar 10 μ m.

REFERENCES

- AMANO, K., & VERMEIJ, G.J., 1998a. Origin and biogeographic history of *Ceratostoma* (Gastropoda: Muricidae). — *Venus, Japanese Journal of Malacology* 57: 209-223.
- & —, 1998b. Taxonomy and evolution of the genus *Ocenebrellus* (Gastropoda: Muricidae) in Japan. — *Palaeontological Research* 2: 199-212.
- BALUK, W., 1995. Middle Miocene (Badenian) gastropods from Korytnica, Poland; Part II. — *Acta Geologica Polonica* 45: 153-255.
- BOUCHET, P., & R. HOUART, 1996. A new genus of Atlantic Muricidae with misleading shell morphology (Mollusca: Gastropoda). — *Journal of Conchology* 35: 423-426.
- CARRINGTON, A.J., & B.F. KENSLEY, 1969. Pleistocene molluscs from the Namaqualand coast. — *Annals of the South African Museum* 52: 189-223.
- COSSMANN, M., & M.A. PEYROT, 1924. Conchologie Néogénique de l'Aquitaine. — *Actes de la Société linnéenne de Bordeaux* 75 (2): 71-144.
- D'ASARO, C.N., 1991. Gunnar Thorson's worldwide collection of prosobranch egg capsules: Muricidae. — *Ophelia* 35: 1-101.
- DEVRIES, T.J., 1997. A review of the genus *Chorus* Gray, 1847 (Gastropoda: Muricidae) from western South America. — *Tulane Studies in Geology and Paleontology* 30: 125-145.
- DEVRIES, T.J., & G.J. VERMEIJ, 1997. *Herminespina*: new genus of Neogene muricid gastropod from Peru and Chile. — *Journal of Paleontology* 71: 610-615.
- GLIBERT, M., 1952. Faune malacologique du Miocène de la Belgique II. Gastropodes. — *Mémoires de l'Institut Royal des Sciences Naturelles de Belgique* 121: 1-197.
- HOUART, R., 1995. *Pteryarchia* n. gen. and *Vaughtia* n. gen., two new muricid genera (Gastropoda, Muricidae: Muricinae and Ocenebrinae). — *Apex* 10: 127-136.
- , 1996. Les Muricidae d'Afrique Occidentale — I. Muricinae & Muricopsinae. — *Apex* 11: 95-161.
- , 1997. Les Muricidae d'Afrique Occidentale — II. Ocenebrinae, Ergalataxinae, Tripterotyphinae, Typhinae, Trophoninae & Rapaninae. — *Apex* 12: 49-91
- JOUSSEAUME, F.P., 1880. Division méthodique de la famille des Purpuridae. — *Le Naturaliste* 3: 367.
- , 1882. Étude des Purpuridae et description d'espèces nouvelles. — *Revue et Magasin de Zoologie Pure et Appliquée* (3) 7: 314-348.
- KENSLEY, B., & J. PETHER, 1986. Late Tertiary and Early Quaternary fossil Mollusca of the Hondeklip area, Cape Province, South Africa. — *Annals of the South African Museum* 97: 141-225.
- KOOL, S.P. 1993. The systematic position of the genus *Nucella* (Prosobranchia: Muricidae: Ocenebrinae). — *Nautilus* 107: 43-57.
- MARKO, P.B., & VERMEIJ, G.J. in press. Molecular phylogenetics and the evolution of labial spines among eastern Pacific ocenebrine gastropods. — *Molecular Phylogenetics and Evolution*.
- MCLEAN, J.H. 1995. Four new genera for northeastern Pacific Prosobranch gastropods. — *Nautilus* 108: 39-41.
1996. Taxonomic atlas of the benthic fauna of the Santa Maria Basin and Western Santa Barbara Channel. Vol. 9 — The Mollusca Part 2 — The Gastropoda — The Prosobranchia. — Santa Barbara Museum of Natural History: 1-160.
- VERMEIJ, G.J., 1993. *Spinucella*, new genus of Miocene to Pleistocene muricid gastropods from the eastern Atlantic. — *Contributions in Tertiary and Quaternary Geology* 30: 19-27.
- , 1995. Morphology and possible relationships of *Ecphora* (Cenozoic Gastropoda: Muricidae). — *Nautilus* 109: 120-126.
- , 1998. New genera of Cenozoic muricid gastropods, with comments on the mode of formation of the labral tooth. — *Journal of Paleontology* 72: 855-864.
- , & R. HOUART, 1996. The genus *Jaton* (Muricidae, Ocenebrinae), with the description of a new species from Angola, West Africa. — *Iberus* 14: 83-91.

- , & E.H. VOKES, 1997. Cenozoic Muricidae of the western Atlantic region. Part XII — The subfamily Ocenebrinae (in part). — *Tulane Studies in Geology and Paleontology* 29: 69-118.
- VOKES, E. H. 1964. Supraspecific groups in the subfamilies Muricinae and Tritonaliinae (Gastropoda: Muricidae). — *Malacologia* 2: 1-41.
- VOKES, E.H., 1971. Catalogue of the genus *Murex* Linné (Mollusca: Gastropoda); Muricinae, Ocenebrinae. — *Bulletins of American Paleontology* 61: 1-141.
- , 1972. *Pteryopsis*, new genus of Trophoninae (Gastropoda). — *Bulletin de l'Institut Royal des Sciences Naturelle de Belgique, Sciences de la Terre* 48: 1-7.