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ORIGINAL ARTICLE

Klaus Bandel · Thorsten Kowalke

Gastropod fauna of the Cameroonian coasts

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Abstract Eighteen species of gastropods were encountered living near and within the large coastal swamps, mangrove forests, intertidal flats and the rocky shore of the Cameroonian coast of the Atlantic Ocean. These represent members of the subclasses Neritimorpha, Caenogastropoda, and Heterostropha. Within the Neritimorpha, representatives of the genera *Nerita*, *Neritina*, and *Neritilia* could be distinguished by their radula anatomy and ecology. Within the Caenogastropoda, representatives of the families Potamididae with *Tympanotonos* and Planaxidae with *Angiola* are characterized by their early ontogeny and ecology. The Pachymelaniidae are recognized as an independent group and are introduced as a new family within the Cerithioidea. Littorinimorpha with *Littorina*, *Assiminea* and *Potamopyrgus* as well as Neogastropoda (*Thais*) and Heterostropha (*Melampus* and *Onchidium*) are described and compared with representatives of the Caribbean and Indo-Pacific province.

Key words Gastropods · Mangrove · Cameroonian coast

Introduction

Between the slope of Mount Cameroon south of Limbe and the forest region at the mouth fo the Sanaga River, an almost uninterrupted zone of mangrove forests is developed, with mud flats at the mouths of the rivers Mungo near Tiko, Wouri in Douala and the Sanaga at Mouanko (Fig. 1). Mangrove and mud flats grade right into volcanic rock beach near Limbe and at Mabeta and are protected by a continuous sand bar in front of the Sanaga delta, while the delta region opens to the sea offshore of Douala. During low tide, the mangrove becomes dry and usually rather wide mud flats and muddy sand flats become exposed. During high tide, most of the mangrove is flooded up to the point where the influence of salty water ends, and the flora is that of a freshwater regime.

With the influence of brackish water, the number of individuals of gastropod fauna increases as well as the number of species, and changes in composition occur. Upstream of Douala harbour and on the flats that lead to the mangrove forest next to Douala airport the beach is covered with much driftwood and rubbish that lies on the landward side of the mangrove forest. Here, *Melampus liberianus* and *Neritina rubricata* are found as well as the *Pachymelania fusca* variety with granulated sculpture that closely resembles *Melanoides tuberculata* in shell shape. These three species move about on the moist surfaces even when not covered by water. In the mangrove consisting predominantly of *Rhizophora* and *Avicennia*, the *Pachymelania fusca* population with varieties having granulated sculpture gradually grades into the population with varieties usually bearing spiral keels. This displays individuals with a variety of ornaments usually dominated by spiral keels in the later whorls. The individuals move about on the mud, feeding when water has run off the tidal flats, and they rest when they are covered by water. Where freshwater seeps from the ground the small variety of *Neritina afra* is common, usually having the shell covered by mud. In areas with soft mud *Tympanotonos fuscatus* with strong nodulation is found, and more rarely also *Tympanotonos fuscatus* variety *radula* with less nodulation appearing during production of the later ontogenetic shell.

Pachymelania aurita prefers the sandy and muddy flats in front of the mangrove, being dominant on sandy flats and less so on more soft muddy flats. Here, on muddy grounds, *Pachymelania fusca* is more common, which usually has a shorter shell than its companion. *Pachymelania aurita* is not only larger than *P. fusca*, but also active when covered by water during high tide as well as when water has run off during low tide. *P. fusca*, in contrast, moves about only on the exposed mud flats

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K. Bandel · T. Kowalke (✉)
Geologisch-Paläontologisches Institut und Museum,
Bundesstrasse 55, D-20146 Hamburg, Germany
e-mail: kowalke@geowiss.uni-hamburg.de

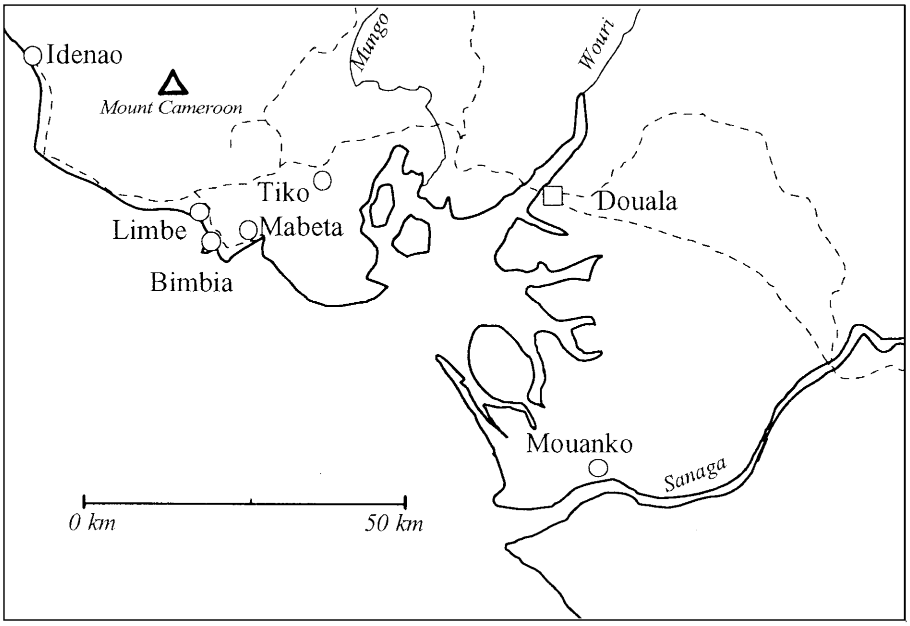


Fig. 1 Location map of explored area on northern coast of Cameroon

and rests when covered by the flood. *P. aurita* prefers water with salt concentrations closer to those of the open sea and plows through the sediment when covered by water, while it moves about on the surface of the bottom when exposed at low tide. On first sight, *Pachymelania aurita* closely resembles *Tympanotonos fuscatus*, even though the latter grows to a larger size and has a larger apical angle. Upon closer inspection the round operculum and the granular ornament of *T. fuscatus* are distinctive. *T. fuscatus* is usually missing from the more sandy areas of the intertidal mud flat, but may be common on the more muddy areas. It may be covered by barnacles when fully grown, while barnacles are rare on the other gastropods of the mud flats. On the mud flats, shells of *Tympanotonos* and *Pachymelania* are commonly encountered in which the latest whorls have been cracked open. This illustrates that predation of the intertidal gastropods by fish and crabs is severe. The presence of spiral and granular enforcements of the shell in addition to a thick shell wall in all species found here is thus explained.

In the mangrove near Tiko to the north of Douala, as well as behind the sand bar in the Sanaga delta to the south of Douala, the supratidal driftwood, in addition to *Neritina rubricata*, *Pachymelania fusca* with fine granulated sculpture and *Melampus liberianus*, is also settled by *Assiminea hessei*. The lower sand flats in the Sanaga estuary have no *Pachymelania aurita*, but many *Thais* cf. *fucus* and *Potamopyrgus ciliatus*. On sandy steep beaches a little further down from the uppermost tidal zone the colorful *Neritina glabrata* lives here among organic debris on wet sand.

The *Nypa* mangrove at Limbe is settled by many *Tympanotonos fuscatus*, all of which have the granulated sculpture, along with *Neritina afra* and *Thais* cf. *fucus*. On the mangrove flats near Tiko *Tympanotonos fuscatus* with coarse granulation may form monospecific populations; at other places in the general area it occurs together with the variety with fine granulated sculpture without intermediate individuals. Thus, it appears in the field, as if both are separate species. *Thais* cf. *fucus* also lives on the rocky shore close to the mangrove area and close to river mouths. Where mud is less abundant in tidal pools, as in Limbe and north of it along the volcanic rock coast of the base of Mount Cameroon, *Angiola lineata* is present as well as a *Petaloconchus* and the tidal zone into the splash zone is settled by *Littorina* and *Nerita*. *Littorina scabra angulifera* is usually present in the mangrove bushes and trees especially at the seaward margin of mangroves.

In the mouths of small rivers coming from the slopes of Mount Cameroon there is usually a sand bar, which creates an estuarine pond with freshwater issuing into it at the landward side and seawater entering it across the sand bar at highest tide on the seaward side. Here, *Neritilia manoeli* is common as well as *Neritina afra*. On drowned logs beside these *Assiminea* is also found. *Neritina afra* of the larger variety produces white egg capsules attached to rocks and pebbles at the end of these ponds, in that portion in which seawater no longer influences salinity and freshwater conditions are present throughout. Sand on the inside of the beach bar that closes the estuarine ponds is the settling ground for young *Tympanotonos* and *Pachymelania*, even though these usually do not grow to adulthood in these environments.

Materials and methods

During a field trip in February 1998, the coastal area of north-west Cameroon between Mount Cameroon and the Sanaga delta was investigated with regard to the gastropod assemblages of the mangroves and estuaries as well as of the rocky shores. The gastropods were studied within their habitats to explore their ecology. Several hundred shells of 18 species reflecting all developmental stages were collected in order to characterize the ontogeny and conchological variability of representatives of the Neritimorpha, Caenogastropoda and Heterostropha.

Juvenile shells were extracted from silty and muddy sediments by sieves. For investigation of the protoconchs (embryonic and larval part of the shell), juvenile shells were mounted on stubs, sputter-coated with gold and documented by scanning electron microscopy (CamScan). Radulae were extracted by dissolving the buccal mass with potassium hydroxide solution and documented by SEM.

Voucher material is deposited at the Geologisch-Paläontologisches Institut und Museum (GPIuM), Hamburg.

Results

Subclass Neritimorpha Golikov and Starobogatov, 1975 – Superfamily Neritoidea Rafinesque, 1815

Family Neritidae Rafinesque, 1815

Within the family Neritidae we found representatives of the genera *Nerita*, *Neritina* and *Neritilia*. Cameroon has a *Nerita* sp. with an up to 12-mm-high and 15-mm-wide shell that lives on the rocky shore within the tidal area and in the splash zone. This species belongs to the subgenus *Nerita* (*Amphinerita*) Martens, 1887 and resembles the type species *N.* (*A.*) *umlaasiana* (Krauss, 1848) from South Africa, but the protoconch is unknown. The teleoconch whorls are ornamented with fine spiral lirae. The outer lip is crenulated with low ridges continuous into the shell's interior. It tolerated quite an amount of freshwater and is found close to river mouths along the shore of Limbe and the base of Mount Cameroon, but it is also present under quite normal marine conditions. The white capsules of its spawn are found under stones and in crevices wherever *Nerita* is found in larger number. The capsule surface holds calcareous spherules, as described by Bandel (1982, 1991). The genera *Neritina* and *Neritilia* produce spawn in their living environment, usually freshwater, and capsule-covers here may only include agglutinated sediment. From this spawn, veliger larvae hatch and leave for the sea. Here, they develop as planktotrophic veligers up to the stage of metamorphosis which is carried out within the estuarine environment as is characteristic of this group (Bandel and Riedel 1998). We observed egg capsules in most landward regions dominated by freshwater influence within the estuarine basal pools formed by the small rivers at the base of Mount Cameroon. These rivers are almost dry in February, with subsurface water running in their pebble beds issuing in the final pool formed by the lowest portion that is separated from the sea by a sand bar. Only at the highest flood does seawater enter these pools which therefore are filled with freshwater most of the time. However, oysters as well as serpulid worms demonstrate that seawater enters these estuarine ponds rather regularly. There are two West African species with rather large and characteristic shells which we did not encounter in Cameroon. Among these, *Neritina oweniana* Wood, 1828 has a wing-like outer lip when fully grown. It lives in nearly normal freshwater (Brown 1980: Fig. 17a,b). *Neritina tiassalensis* Binder, 1955 lives in streams of the Ivory Coast. It is also rather large (more than 20 mm in diameter) and lacks the extended aperture.

Subfamily Neritininae Rafinesque,1815 – Genus Neritina Lamarck, 1816

Species Neritina afra *Sowerby, 1841*. The shell of *Neritina afra* Soverby, 1841, measuring up to 14 mm in height and 13 mm in width, has a low though distinct spire and coarse teeth on the columellar plate (Brown 1980: Fig. 18d,e). Coloration is dark greenish-brown, but some juveniles have large yellowish patches. The columellar plate has a distinct faintly orange tinge. Individuals of this species are present in the upper tidal mud flats of the *Nypa* mangrove near Limbe as well as in the estuarine pools of the small rivers that issue into the sea at Mount Cameroon between Limbe and Idenao. Freshly metamorphosed young have been noted to be present on all kinds of hard substrates found in the estuarine pools, in especially great numbers near its margin with the continuous freshwater environment and near springs in the gravel bed. The adults work their way upriver and produce egg capsules, coating the rocky river pools within the zone of pure freshwater influence. *Neritina afra* at the base of Mount Cameroon occurs together with *Neritilia manoeli*. The dull colored *Neritina* which occurs commonly in the upper tidal flats in and outside the mangrove swamps wherever freshwater seeps out of the ground may also represent *N. afra*, even though it remains of smaller size. Large populations have been encountered near Limbe, Tiko, and the Wouri estuary of Douala. Radulae of both ecological variants are identical in shape, and the specimens of larger size could only be found in the river mouths. If both forms belong to the same species, this may indicate that they only grow to adulthood and reproduce when they are mainly exposed to freshwater and do not reach maturity when the freshwater influence decreases.

Juvenile individuals of *N. afra* are more colorful than older ones and, thus, resemble *N. glabrata* from the Sanaga delta. However, members of both species can be well distinguished by the radulae (Fig. 2a,b), since the rachidian tooth of *N. afra* in contrast to that of *N. glabrata* is more high than wide. The outer laterals bear about 15 small denticles in the case of *N. afra* and about 6 coarse denticles in the case of *N. glabrata*. The inner marginals have slender elongated denticles in *N. afra* and shorter coarse denticles in *N. glabrata*.

Species Neritina glabrata *Sowerby, 1849.* The up to 7.5-mm-high and 8.5-mm-wide shell of *Neritina glabrata* Sowerby, 1849, is smooth and has a low spire and evenly rounded last whorl. The ornament is highly varied (Pilsbry and Bequaert 1927). According to Brown (1980: Figs. 18b,c), *N. glabrata* is abundant in brackish water in estuaries and lagoons on sand, rock and vegetation from Gambia to Angola. This commonly bright yellow species has also a rather large variety of ornaments consisting of

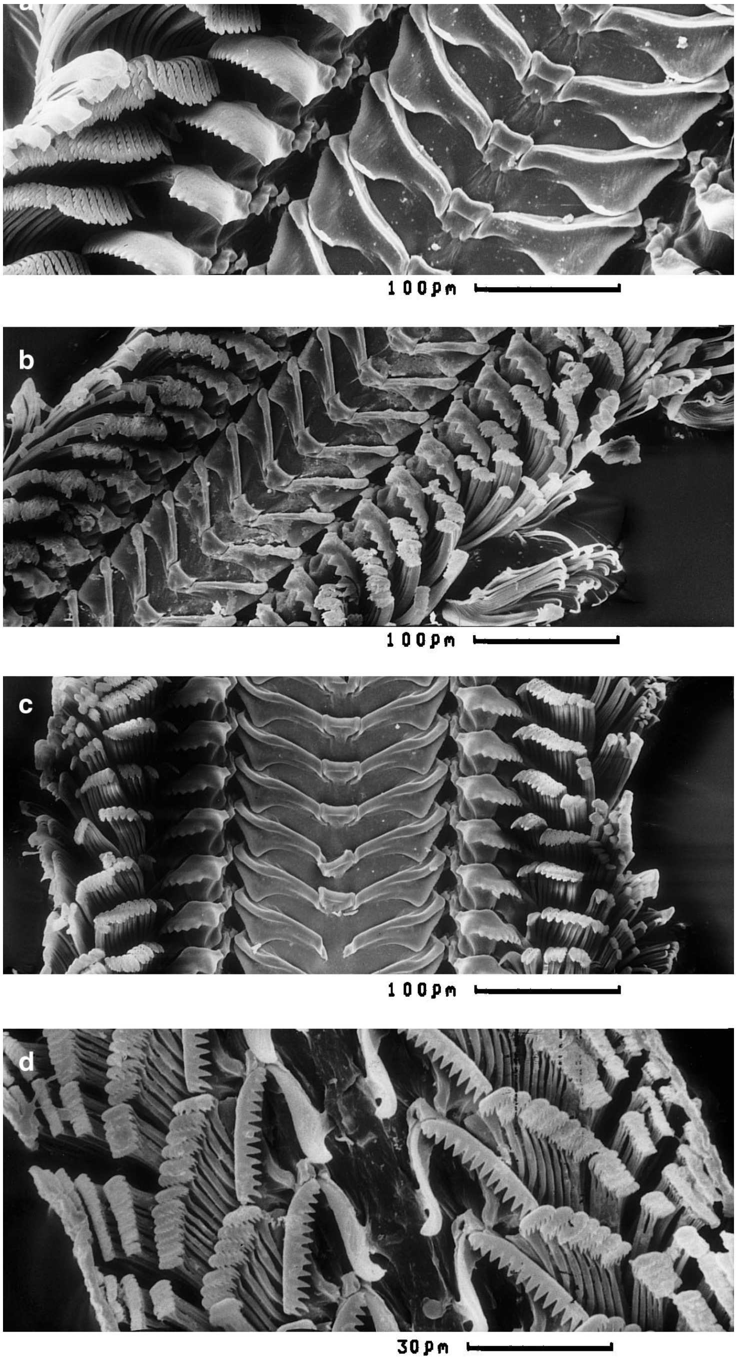


Fig. 2 Radula of **a** *Neritina afra* Sowerby, 1841, from an upper tidal mud flat of *Nypa* mangrove at Limbe; **b** *Neritina glabrata* Sowerby, 1859, from beach rubble at the estuary of the Sanaga River; **c** *Neritina rubricata* Morelet, 1858, from driftwood of uppermost tidal zone at estuary of Wouri River; **d** *Neritilia manoeli* Dohrn, 1866, from a stream north of Limbe

stripes and dots in several colors. It is very common on the beach in the coastal lagoon at the Sanaga river delta. It is more colorful and has a less expanded spire as well as a narrower aperture than *N. afra* and is also distinctive regarding the radula (Fig. 2b). Also, *Neritina glabrata*'s place on the coast differs by being found on more beach sand and beach rubble with water seeping through in contrast to the sandy muddy mangrove flats in the uppermost tidal regime where *N. afra* is found. Its bright coloration and place in the estuary near to the sea resembles the Indo-Pacific *Clithon oualaniensis* Lesson, 1831 as described by Bandel and Riedel (1998).

Species Neritina rubricata *Morelet, 1858. Neritina rubricata* Morelet, 1858, measures up to 13 mm in height and 12 mm in width. It lives on the underside of wet logs in the beach drift of the uppermost tidal zone in the mangrove environment. The dull colored shell has a prominent spire in contrast to *N. afra* and *N. glabrata* and a toothed columellar margin. *N. rubricata* can also be distinguished by radula characteristics. The radula (Fig. 2c) resembles that of *N. glabrata*, but differs regarding the shape of the central tooth which is more wide than high and more elongated than in *N. glabrata*. The outer lateral teeth are characterized by nine coarse denticles and, thus, more than are present in *N. glabrata*. The denticles of the inner marginal teeth are also shorter than those of *N. glabrata*. According to Mandahl-Barth (1973) and Brown (1980: Fig. 17d–f), *N. rubricata* is found from Gambia to Cameroon. It occurs in more hidden environment, but was encountered at the Sanaga delta, the estuary of the Wouri River and further to the north near Tiko. This species lives and is active in moist environments far up the beach and rests when covered by water.

Subfamily Neritiliinae, Baker 1923 – Genus *Neritilia* Martens, 1879

The genotype is *Neritilia rubida* (Pease, 1865) from Tahiti. All species belonging to this genus are small (2–4 mm voide) and have an obliquely egg-shaped, subglobular shell which is smooth and has a semicircular oblique aperture. Its inner lip is formed by a narrow callus and a smooth columellar margin. The operculum of *Neritilia* has a simple apophysis. The radula of *Neritilia rubida* lacks a central tooth, and there is only one intermediate tooth on both sides with a lenticular form, inclined anterior edge and a short outer lappet. The lateral tooth has an inclined cutting edge with 12–14 denticles and a rounded outer basal projection. The marginal teeth broaden at their anterior end and carry 4–5 denticles here. According to Starmühlner (1983), the shell of *Neritilia consimilis* (Martens, 1879) is obliquely elliptical and not transversely ovate as in *Neritilia rubida*. Also, the aperture of *N. consimilis* is oblique and semi-elliptical and not extended as in *N. rubida*. The radula of *N. consimilis* from Madagascar, Mauritius, the Comores and Seychelles has been described by Baker (1923) and Starmühlner (1976, 1983, 1993). Here, the lateral tooth posesses 8–12 denticles on the cutting edge and the marginal teeth have 5–6 denticles. Starmühlner (1986) considered *N. consimilis* and *N. rubida* to be closely related species but distinct from each other even though both live in very much the same type of environment.

Species Neritilia manoeli *Dohrn, 1866*. The small shell of *Neritilia manoeli* Dohrn, 1866, measures up to 3.5 mm in height and 4 mm in width. Its shape is oval, egg-like and with a convex apical side. Juvenile stages have yellowish coloration while older individuals are brownish or have a black outer layer. The aperture is semicircular and wide with a callus of the inner lip and a nondented columellar lip (Brown 1980: Fig. 18f; Starmühlner 1993: Plate 14, Figs. 158–160). The operculum is thin with a reddish inner and outer side. A thin appendage (peg) is present on the inner side which is simple and extends over the edge. The analysis of the radula confirmed that the typical feature of the genus consisting of the absence of a central tooth is correct (Fig. 2d). The outer lateral tooth with its cutting edge bearing 13 denticles is very similar to that of the type, *N. rubida*. However, in contrast to *N. rubida*, the marginal teeth bear eight denticles. *N. manoeli* also differs from *N. consimilis* from Madagascar as well as from the South African Umzamba estuary by bearing eight denticles on the cutting edge of the marginals. *N. succinea* Recluz, 1811 from the Republic Dominica is distinctive by its lateral teeth bearing 15 denticles and marginals with 10 denticles on the cutting edge.

We found *Neritilia manoeli* in the streams that come from Mount Cameroon north of Limbe living on aquatic plants, wood and rocks within the upper portion of estuarine ponds. Boettger (1905) had found individuals of this species in similar occurrences.

Subclass Caenogostropoda Cox, 1959 –
Order Cerithiimorpha Golikov and Starobogatov, 1975 –
Superfamily Cerithioidea Férussac, 1819

Family Pachymelaniidae fam. nov.

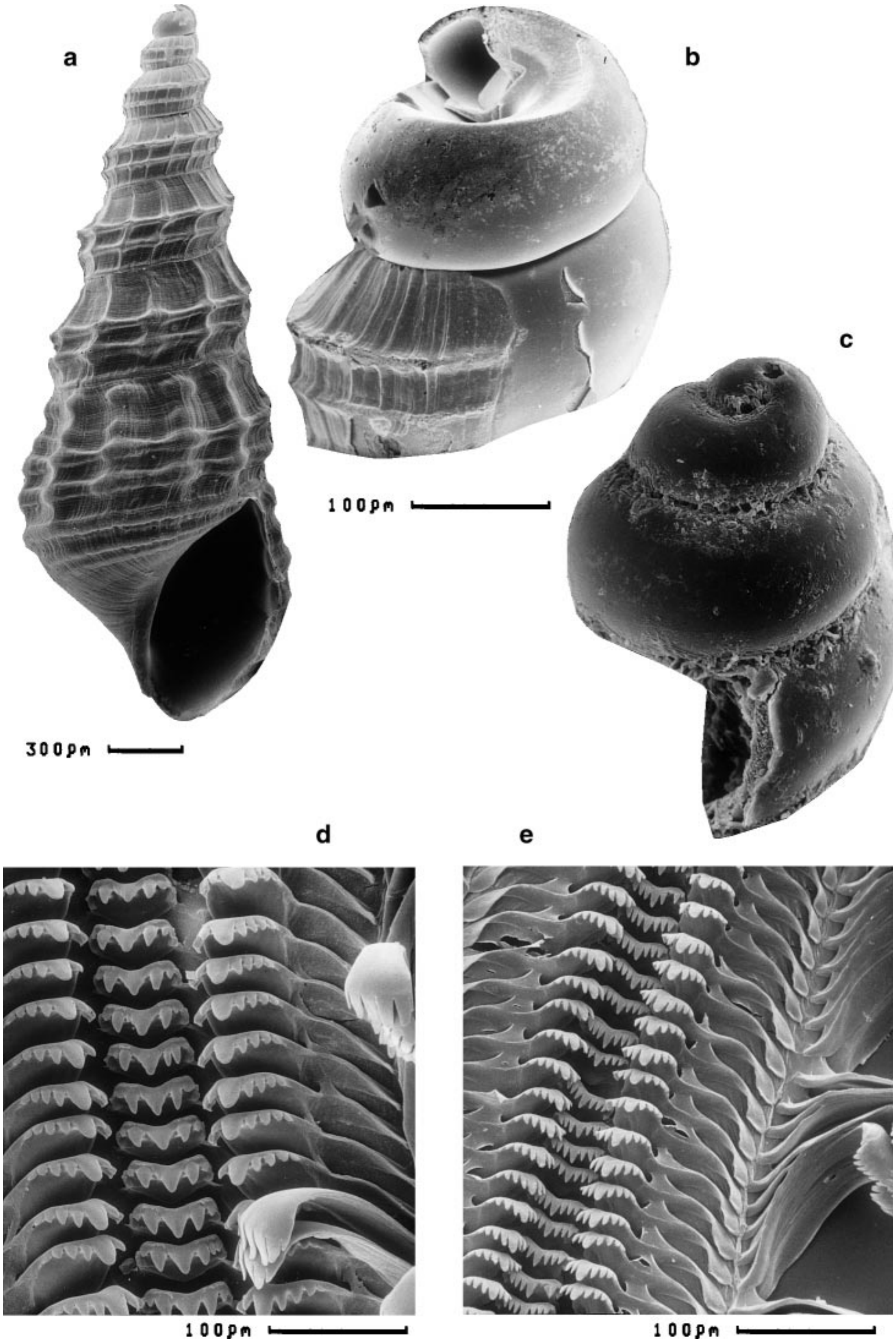
The family holding the surviving genus *Pachymelania* with its three species comprises large, up to 60-mm-high brackish water gastropods with an elongated, commonly decollated spire and strong axial and spiral sculpture. The shape of the aperture is ovate to subangular with a slight narrow anterior canal and a broad basal notch. The inner lip is callus covered. The paucispiral operculum is characterized by a nucleus near the base. The protoconch formed by the planktotrophic veliger is smooth, slender, and comprises several whorls.

The teleoconch distinguishes the Pachymelaniidae from the Melanopsidae, which lack spiral sculpture. The smooth protoconch distinguishes Pachymelaniidae from the larval shell of Potamididae which is characterized by strong spiral ornament (Kowalke 1998). Potamididae like *Tympanotonos* also have a multispiral operculum with a central nucleus while that of the Pachymelaniidae is paucispiral with acentric nucleus. Among the Thiaridae, *Melanoides* sometimes has a very similar appearance to that of the teleoconch, but the family is distinctive regarding their anatomical features, including a brood pouch in the head-foot, while Pachymelaniidae have an ovipositing groove on the foot and lay eggs within gelatinous masses on the muddy ground. The protoconch of Thiaridae with planktonic larval development differs by its ornamented larval shell (Bandel and Riedel 1998).

Genus *Pachymelania* E. Smith, 1893

The type species fo the genus *Pachymelania* E. Smith, 1893, is *Pachymelania byronensis* Wood, 1818 from Guinea, representing a species with a double row of nodules on its whorls (Brown 1980: Fig. 53a). Plaziat (1977) found all three existing *Pachymelania* species on the tidal flats of Douala. We found *P. byronensis* only occupied by hermit crabs but the other two species alive in large numbers.

Fig. 3 **a** Juvenile specimen of *Pachymelania aurita* Müller, 1774, from a sandy intertidal flat of estuary of the Wouri River; **b** larval shell and early teleoconch of *P. aurita* from estuary of Wouri River. Transition to teleoconch is slightly sinuous. **c** Protoconch of *P. aurita* from the estuary of the Wouri River with preserved embryonic shell; **d** radula of *Pachymelania fusca* Gmelin, 1791, from uppermost tidal zone of estuary of Sanaga River; **e** radula of *Pachymelania aurita* from a sandy intertidal flat of estuary of Wouri River



Species Pachymelania aurita *(Müller, 1774).* The shell of *Pachymelania aurita*, Müller, 1774, reaches 55 mm in height. A single row of stout tubercules dominates the ornament of lower whorls, while the upper whorls bear ribs and spiral keels (Brown 1980: Fig. 53b; Fig. 3a). *P. aurita* represents an extremely common species in the estuary of the Wouri River at the seaward side of Douala harbour. Here, it occurs on the open muddy and sandy intertidal flats jointly with *Tympanotonos* and *Pachymelania fusca*. At first sight, *P. aurita* closely resembles *Tympanotonos*, but its spiral angle is smaller and the operculum not round as in the latter. The sexes are separate, as documented by Ajao and Fagade (1990). A spawn-conducting groove is present on the foot of the female. According to Ajao and Fadage (1990), the fertilized ova are spawned, and planktotrophic larvae develop in Lagos/Nigeria. However, actually the larval shell of any *Pachymelania* sp. from West Africa has not been described to date.

In the radula of *P. aurita* (Fig. 3e) the central tooth is as high as it is wide, not wider than high as is the case in the known radulae of thiarids (Bandel et al. 1997). The lateral teeth lack small denticles on a rounded extension next to the central tooth. In contrast to the radula of the genus *Melanopsis* (Melanopsidae), in *Pachymelania* the central tooth lacks a median swelling and basal extensions. The barrel-shaped protoconch consists of 2.75–3 smooth whorls reaching 0.34 mm in height (Fig. 3b,c). The first whorl measures 0.11 mm in maximum diameter and the initial cap of the embryonic shell is 0.03 mm wide. The transition to the teleoconch is only slightly sinuous, and its onset is indicated by the appearance of two spiral keels and weak axial riblets.

In contrast to potamidid larval shells, that of *P. aurita* is not ornamented but smooth. It was not possible to demarcate the embryonic and larval shell, but the transition should lie in the region of growth-line insertion. However, the dimensions of the initial whorl are indicative of a small planktotrophic veliger hatching from the spawn. The protoconch dimensions provide evidence of a long stay within the plankton, probably longer than suggested by Ajao and Fagade (1990) who mentioned a time of 7–8 days in the plankton without stating from which source they extracted their data.

The protoconch of a species described as *Harrisianella vulcani* Brongniart, 1823 (Szöts 1953: 166, plate 4, Figs. 1–3) from the Middle Eocene of Gant (West Hungary) is very similar regarding the larval shell. Since teleoconch shape of this species also fits well with *Pachymelania*, *H. vulcani* probably represents an early species of the family that lived in a mangrove environment of the northern Tethys together with *Tympanotonos* spp. The modern West African mangrove community could, thus, be interpreted to represent a relict population of the coastal region of the former Tethys Ocean.

Species Pachymelania fusca *Gmelin, 1791*. Within the estuary of Wouri and Sanaga rivers in Cameroon, *P. fusca* Gmelin, 1791, is extremely common in mangrove swamps as well as on intertidal flats. Where the influence of freshwater is low in mangrove surroundings, as found near Tiko and Limbe, the species is absent. The shells, measuring up to 45 mm in height, have a highly variable ornament (Brown 1980: Fig. 53c,d), and there is also quite some variation regarding shell size and spire angle. The species is always smaller than *P. aurita*, and there are no transitions to it. The radula differs from that of *P. aurita* by bearing fewer denticles on the rachidian tooth (Fig. 3d). The denticles are coarser, with the median denticle not being as elongated as in *P. aurita*. Spawn consists of short packages of gelatinous egg mass consisting of round egg capsules in a jelly mass, and each egg capsule holding one greenish embryo. This develops within the egg yolk into a planktotrophic veliger. The egg mass is deposited in short gelatinous ribbon segments consisting of some 20–50 egg capsules surrounded by a gelatinous mass. Regarding the deposition of the eggs in the sediment, *Pachymelania fusca* resembles *Melanopsis*, which has the same strategy. Different morphs of *P. fusca* have been described by Pilsbry and Bequaert (1927) from the estuary of the Congo River. Binder (1957) described the variation along the Ivory Coast.

Ecologically, the morph of *Pachymelania fusca* which remains *Melanoides*-like (form "*granulosa*" according to Pilsbry and Bequaert 1927) in shell shape throughout its life differs from the *P. fusca* with spiral ribs by living within the uppermost shore and remaining active and moving about even when the ground is almost dry. It does not represent an independent species because transitional forms exist, but it does represent an ecologically independent branch of a species in which mode of life and shell shape differ from the morph that lives on wet muddy ground further toward the sea. Analyses of the radulae of different morphs yielded no differences and confirmed the existence of a single species, *P. fusca*.

Family Potamididae H. and A. Adams, 1854

The family name Potamididae H. and A. Adams, 1854, is based on *Potamides* Brogniart, 1810, with the type *P. lamarcki* Brogniart from the Oligocene of south-western Germany. Thiele (1929) differentiated Cerithioidea of the tropical coastal swamps into the Potamididae and Batillariidae. This was confirmed by Houbrick (1991) who had revised most members of these two families. The family Potamididae comprises medium- to large-sized snails reaching 20 cm in height with high spire and commonly strong sculptures. The aperture has a deep notch at its base and the operculum is multispiral and corneous. Brown (1980) reported the presence of the four genera *Cerithidea*, *Terebralia*, *Tympanotonos* and *Pirenella* from Africa. *Pirenella* actually represents a synonym of *Potamides* (cf. Kadolsky 1984; Kowalke 1998). Houbrick (1984, 1988, 1991) suggested that the Potamididae represent a monophyletic group within the Cerithioidea. However, Houbrick (1991) also pointed out that the exact phylogenetic relationship of *Telescopium* and *Terebralia* to the genera *Cerithidea*, *Potamides* and *Tympanotonos* has not been ascertained by anatomical studies up until now.

With regard to the shell shape, the outline of the outer apertural lip of fully grown individuals is characteristic. Potamididae represent common intertidal snails with an amphibious existence on muddy habitats confined to tropical and subtropical regions. They settle in mangrove swamps and on salt marshes where they feed on detritus and graze microalgae.

Genus *Tympanotonos* Schumacher, 1817

The type species of the genus *Tympanotonos* Schumacher, 1817, is *T. fuscatus* (Linné, 1758) and it is thought that only one species is present on the West African coast (Brown 1980). Its shell size reaches 80 mm in height. The anatomy was described by Johansson (1956). According to Binder (1957, 1968), Elouard (1974), Elouard and Rosso (1977) and Plaziat (1974, 1977), the species can be found from Senegal to southern Angola. According to Binder (1957), it tolerates freshwater influence to a salinity of about 2 ppt.

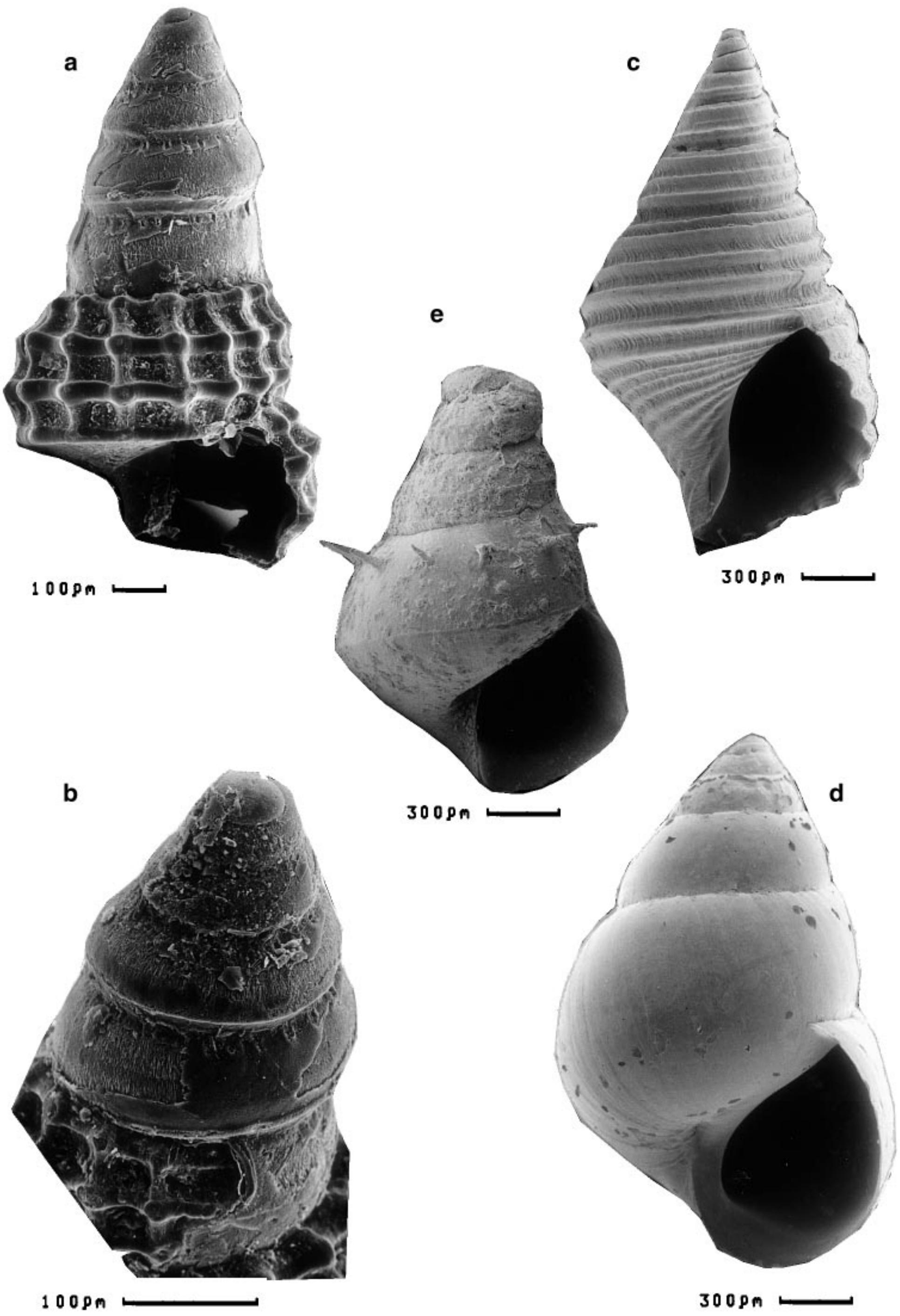


Fig. 4 **a** Juvenile specimen of *Tympanotonos fuscatus* Linné, 1758, from a mud flat of *Nypa* mangrove at Limbe, with slender tower-shaped protoconch and early teleoconch; **b** protoconch of same specimen is sculptured by two spiral keels, a subsutural row of tubercules and is terminated by a strong sinusigera notch; **c** juvenile specimen of *Angiola lineata* da Costa, 1778, from an upper tidal pool of the basaltic rocky shore at Limbe; **d** *Assiminea hessei* Boettger, 1887, from uppermost tidal zone of estuary of Sanaga River; **e** juvenile specimen of *Potamopyrgus ciliatus* Gould, 1850, from a muddy pool of *Nypa* mangrove at Limbe

The species *T. fuscatus* appears in two varieties: that with fine granulation is *T. fuscatus radula*, while that with coarse granulation is *T. fuscatus fuscatus* (Brown 1980). According to our observations, these varieties usually occur in one and the same location in pure forms, and only in one location were they together but well distinguishable. Plaziat (1977: Fig. 8a–c) described a transitional form from Douala with coarse granulation on most of the teleoconch and fine granulation on the last teleoconch whorl. He interpreted the variety with fine granulation as being adapted to lower water energy and the supratidal zone and the variety with coarse granulation as characterizing more turbulent water conditions. This ecological difference could not be verified by us. Analysis of radulae of both varieties yielded no significant differences and radular characters; this would indicate that both belong to one and the same species.

Even though we collected many hundreds of tiny specimens, only one specimen yielded a preserved spire (Fig. 4a,b); in all others it had become dissolved away.

The slender tower-shaped protoconch (Fig. 4b) secreted by a planktotrophic veliger comprises 4.25 whorls measuring 0.53 mm in height. The embryonic shell of about one whorl is smooth, measures 0.96 mm in maximum diameter and has an initial cap that is about 0.05 mm wide. The onset of the larval shell is indicated by the formation of a subsutural row of large longitudinal tubercules. Near the base of the larval whorls two distinct spiral keels cause the angular outline of the whorls. The protoconch terminates with a well-developed sinusigera notch that is thickened in its upper portion and quite thin at its base.

This protoconch is typical of a cerithioidean veliger larva that lives in the plankton for an extended time (Bandel and Riedel 1998; Kowalke 1998). It has a very similar ornament to those of the oldest known representatives of the Potamididae from the Upper Cretaceous (Coniacian) of the Northern Alpine Gosau Formation and to modern *Terebralia palustris* Linné, 1758 from the Indo-Pacific as well (Kowalke and Bandel 1996; Kowalke 1998). In contrast to the West African species *Tympanotonos fuscatus*, the East African species *Terebralia palustris* is characterized by a veliger that swims only for a short time in the plankton, and the embryonic shell here forms a bulbous first whorl, with the larvae adding only another whorl while in the plankton.

The spawn of *Tympanotonos fuscatus* is a narrow meandering ribbon that is attached to hard substrates and is commonly mud encrusted. It consists of many small eggs each held within a round egg capsule. Several such capsules next to each other are agglutinated to each other by a jelly substance and jointly form the narrow ribbon. We found it attached to wood and rocks on the tidal muddy flat of Tiko. It closely resembles the spawn of *Cerithium* and *Batillaria* (Bandel 1975).

The variety with coarse sculpture is also common in the estuarine flats of the harbour of Douala, here together with both species of *Pachymelania*. The variety with granulated sculpture occurs in pure populations in the estuary of the small river that issues into the sea at the fishing market of Limbe. In this *Nypa* mangrove the population co-occurs with *Thais* in the more seaward area and with *Neritina afra* in the more landward area. At the more sea-exposed side, muddy puddles with running water contained many young of the species. In the higher estuary, individuals are usually larger, either half or fully grown specimens, the latter common around the base of the *Nypa* bushes.

Family Planaxidae Gray, 1850

Genus *Angiola* Dall, 1926

On the basaltic rocky shore at Limbe, *Angiola lineata* da Costa, 1778, is common on stones in tidal pools. It tolerates freshwater when living near river mouths as well as water that is strongly warmed up during low tide along this black basaltic shore in the upper tidal pools and splash puddles. The thick-shelled teleoconch reaches a height of 10 mm. comprising up to nine slightly inflated whorls with a variable color pattern. The early whorls of the teleoconch bear strong spiral ribs (Fig. 4c). The sculpture of the later teleoconch is reduced, and the last two whorls may be smooth. Houbrick (1987) described the anatomy in detail.

The protoconch comprises 3.25 whorls and measures about 0.25 mm in height. The initial cap is about 0.03 mm wide, and the first whorl measures 0.9 mm in maximum diameter. The sculpture of the larval shell is not preserved. It probably is the same as that of *A. lineata* from the Caribbean coast of Colombia (Kowalke 1998: Plate 5, Fig. 8), of which hatching mode and embryonic shell have been described by Bandel (1975). The radula of the Caribbean representative of this species has been described by Bandel (1984: 35–36, Fig. 57) and Houbrick (1987: 23, Fig. 16A,C–E). In contrast to species with a known protoconch of the genus *Planaxis*, the larval shell of *Angiola lineata* bears more whorls. *Angiola* also has the ornament of the early teleoconch stronger developed than *Planaxis*. Comparison of protoconch dimensions, sculpture of the early teleoconch and radulae of the Caribbean *A. lineata* and specimens from Limbe revealed that both are quite similar. *A. lineata*, which is widespread in the Caribbean Sea, therefore also lives along the West African coast of Cameroon. It may cross the South Atlantic Ocean by aid of its long-time veligers.

Order Littorinimorpha Golikov and Starobogatov, 1975

Within the family Littorinidae Gray, 1840, we found the West African subspecies *Littorina* (*Littorinopsis*) *scabra angulifera* (Pilsbry and Bequaert, 1927) on the *Nypa* palm and the *Acrostichum* fern within a small mangrove zone near the port of Limbe. According to Brown (1980), *Littorina* (*Littorinopsis*) *scabra scabra* Linné, 1758, is a common species on mangrove trees of the East African shores. *Littorina* (*L.*) *scabra angulifera* has been described from the Miocene of Panama by Woodring (1959). It is also very common in the mangrove around the Caribbean Sea (Bandel and Wedler 1987). Comparative analysis of the radulae of individuals from Limbe and Santa Marta (Colombia) yielded no differences and, thus, confirmed the wide distribution of the subspecies around the tropical South Atlantic Ocean. The genera *Paesiella* Nevill, 1885, *Littoraria* Griffith and Pigeon, 1834 and *Mainwaringia* Nevill, 1885 are adapted to the mangrove environment in the Indo-Pacific region as well as in South America (Reid 1989) with similar ecology.

The family Assimineidae, superfamily Rissooidea, is representated by *Assiminea hessei* Boettger, 1887 (Fig. 4d). According to Brown (1980: Fig. 46b), this species is found in Nigeria together with *Melampus liberianus* in the upper tidal limits of a mangrove swamp. This is also where we found *A. hessei* behind the beach wall that separates the Atlantic Ocean from the mangrove lagoon near the Sanaga River mouth. The species lives on the underside of wet logs in the uppermost tidal regime.

It ecologically differs from a form that lives on pieces of wood in the estuarine pools formed by small rivers at the base of Mount Cameroon, since this species lives in freshwater with brackish intervals, usually submerged. *A. hessei* accompanies *Melampus* and lives mostly on moist surfaces above water.

The up-to-6-mm-high hydrobiid *Potamopyrgus ciliatus* Gould, 1850 (Fig. 4e), as described by Pilsbry and Bequaert (1927) and Brown (1980), is characterized by black spines of periostracum with vertically aligned bases arranged below the sutures. It was first described from Cameroon by Verdcourt (1976), who found the species on the aquatic plant *Jussiaea repens*. We collected specimens from muddy pools of the *Nypa* mangrove near the port of Limbe. The protoconch which is not well preserved seems to reflect an indirect mode of development. It comprises about two whorls. The first whorl measures about 0.1 mm in diameter. The nonspiral initial cap is about 0.03 mm wide. It is ornamented by a groove-ridge pattern. After half a whorl, relics of spiral lines are present. The larval shell is characterized by widely arranged spiral lines.

Order Neogastropoda Thiele, 1929

Within the genus *Thais* Röding, 1798, *Thais* cf. *fucus* Gmelin, 1789 was commonly found feeding on mangrove snails behind the beach wall in the coastal lagoon near the Sanaga River mouth and in the mangrove near Tiko in the larger estuarine area of the Mungo River. It is also common on rocks at Bimbia and Mabeta near Limbe, here feeding on barnacles. A member of the Fasciolariidae comes up into the estuarine area of the beach in Limbe, where the river leaves the *Nypa* growths. We encountered it, but did not take any of the large shells.

Some neogastropod genera entered the mangrove environment in several localities. The genera *Melongena* and *Thais* live in the mangroves of Colombia (Bandel and Wedler 1987). *Nassarius* represents a common faunal element within mangroves of south-eastern Asia, where it even migrated into freshwater in the Mekong area. Other neogastropods living in the mangroves are *Conus* in Cebú, the Philippines, and a columbellid in Bagamoyo, Tanzania. “*Cantharus*” *brongniati* within the Fasciolariidae is an Eocene representative from a coastal swamp of the Northern Tethys of Hungary (Szöts 1953), but it appears that there is no close relation to any modern neogastropod connected to mangrove habitats. These data indicate that the few species of neogastropods living in mangroves seem to belong to different groups, and penetration of these biotopes appears to be only marginal.

Subclass Heterostropha Fischer, 1885

Melampus liberianus H. and A. Adams, 1854 (Ellobiidae) is a common representative of the archaeopulmonates. This species, figured by Brown (1980: Fig. 75e), remains small, measuring up to 14 mm in height. It is usually found on the underside of wet or damp logs in the uppermost tidal area, commonly together with *Neritina rubricata* and *N. glabrata*, *Pachymelania fusca* and *Assiminea hessei*. Another representative of the Archaeopulmonata is an *Onchidium* sp. (Onchidiidae) settling on the rocky shore of Mabeta south of Limbe. The genus *Onchidium* is also present at the East African mangrove, i.e. at Bagamoyo, Tanzania, as well as in the mangroves of Bali, Indonesia.

Within the mangrove of Central America and Brazil, *Blauneria* and *Melampus* are common (Marcus and Marcus 1965; Martins 1995). *Cassidula* and *Pythia* are characteristic genera of the uppermost intertidal zone in the Indo-Pacific region, while *Melampus* and relations also have relatives in the region of West Africa and the Caribbean Sea, all of which are well known by now due to the research carried out by Martins (1995) and Harbeck (1996). Ellobiidae among the Archaeopulmonata have been living in coastal swamp environments since Late Jurassic times (Bandel 1991) and were also recognized here during the Late Cretaceous (Bandel and Riedel 1994).

We also found a representative of the order Opisthobranchia, *Haminoea* sp., living in small tidal pools on the basaltic rocks of the mangrove bay at Mabeta, where it also produces its characteristic collar-like spawn.

Discussion and conclusions

A rather small number of species but connected to a large number of individuals characterizes the gastropod fauna of the Cameroonian mangrove coast and its vicinity along the rocky shore. In this regard the fauna is typical of brackish-water extreme biotopes, being settled by a few species adapted to rapid changes in salinity and water energy, commonly forming mass populations. Analysis of the assemblages yielded interesting data concerning their ecology and early ontogeny, also reflecting systematic implications.

Within the Neritimorpha, *Nerita* sp. is well separated from representatives of the genera *Neritina* and *Neritilia*. *Nerita* lives along the rocky shore near Limbe affected by freshwater of the small streams issuing from Mount Cameroon, but mainly under fully marine conditions. *Neritina* spp., in contrast, need brackish water in their adult lives. *Neritina afra*, being present on mud flats as well as in estuarine pools, and convergent *N. glabrata* from beach rubble could be distinguished by their ecology and also by radula anatomy. *N. rubricata* living in the same biotopes as the latter is easily distinguishable by its prominent spire. *Neritilia* is represented by the single species *N. manoeli*, living mainly under freshwater influence in the upper portion of estuarine ponds. *N. manoeli* could well be differentiated from the East African species *N. consimilis* and the Caribbean *N. succinea* by radula characteristics.

The caenogastropod family Potamididae in Cameroon is represented by the genus *Tympanotonos*. The observations of Plaziat (1977) that just one species with two phenotypes exists can be confirmed. *Tympanotonos fuscatus* morphs with strong nodulation and those with fine granulated sculpture showed no transitional forms, even though it sometimes occurs in one and the same locality. However, comparison of the radulae of both morphs yielded no differences. The protoconch is described for the first time. It is secreted by a long-time veliger and shows the typical potamidid scupture that we know from species as far back as the Late Cretaceous (Kowalke and Bandel 1996; Kowalke 1998). An individual placed in a small aquarium with brackish water survived for almost a year at the GPIuM in Hamburg.

Angiola (Planaxidae) was analysed with regard to the radula anatomy and early ontogeny. It demonstrated great similarities with the Caribbean species *A. lineata* so that it can be regarded as representing the same species. Thus, *A. lineata* also occurs along the West African coast, from where it is reported here for the first time.

The Pachymelaniidae are introduced as new family and placed next to the Melanopsidae and the Potamididae. They were formerly attributed to the Thiaridae or Pleuroceridae. According to Binder (1957) and Brown (1980), radula and operculum are similar to that of *Melanoides*. Wenz (1938–1944) included *Pachymelania* within the Thiaridae following Thiele's (1929) suggestion, as did Brown (1980). Morrison (1954) included *Pachymelania* with the Pleuroceridae. Analysis of their anatomy confirmed the absence of a brood pouch and the deposition of spawn on the muddy ground. Differences concerning radula morphology supported evidence of a systematic placement outside of the Thiaridae. The new data concerning protoconch morphology also indicate an independent branch of cerithioidean evolution. Radula and operculum morphology indicated some relationship with the Melanopsidae, which could also be verified by RNA analysis (R. Bischoff, Bremen, personal communication). However, according to these later data, the Potamididae are also a potential sister group, and all three together, Pachymelaniidae, Potamididae and Melanopsidae, jointly differ from the other Cerithioidea. *Pachymelania aurita* and *P. fusca* could be confirmed as separate species, being ecologically and anatomically distinct and showing no transitions. *P. fusca* is present in two morphs which are connected by a transitional form. *P. fusca*, with its characteristic spirally keeled sculpture, is present on wet mud flats affected by each tide, living under quite marine conditions. The morph with fine granulated sculpture characterizes the uppermost shore, remaining active when the ground is almost dry. Some individuals of this morph could be kept alive in aquaria in pure freshwater for about 1 year.

Littorinimorpha are represented by *Littorina* (*Littorinopsis*) *scabra angulifera* (Littorinidae) living on mangrove trees, and show no differences to the form living in the Caribbean region. The identity of representatives of the subspecies could also be verified by a comparative analysis of the radulae of specimens from both localities. *Potamopyrgus ciliatus* (Hydrobiidae) and *Assiminea hessei* (Assimineidae) are small rissooids characterizing shallow muddy habitats and the uppermost shore, where they live jointly with achaeopulmonates of the genera *Melampus* (Ellobiidae) and *Onchidium* (Onchidiidae). Within the Neogastropoda, *Thais* cf. *fucus* (Thaididae) and a fasciolariid prey on other mangrove molluscs. The latter is only rarely distributed and seems to be restricted to the *Nypa* mangrove near Limbe, being only marginally connected to the mangrove environment. *Thais* cf. *fucus*, in contrast, is a typical mangrove species, being abundant in all types of mangroves affected by a wide range of salinity.

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