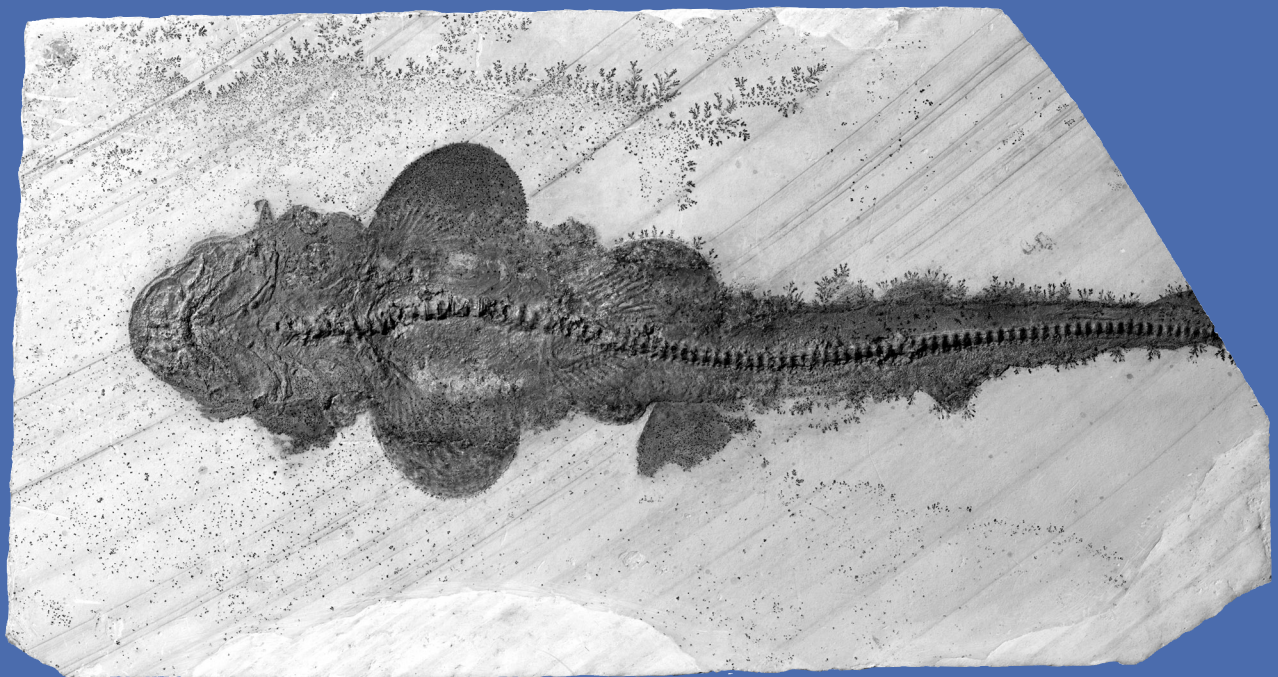


Zitteliana

An International Journal
of Palaeontology and Geobiology

Series A/Reihe A
Mitteilungen der Bayerischen Staatssammlung
für Paläontologie und Geologie

44



München 2004

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EDITORIAL NOTE

As of in 2003, the journal *Zitteliana* is published in two series.

Series A: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie (ISSN 1612-412X) replaces the former „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). The numbering of issues is continued (last published: Heft 43, 2003).

Series B: Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie (ISSN 1612-4138) continues the previous „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627).

Instructions for authors are included at the end of this volume.

HINWEIS DES HERAUSGEBERS

Vom Jahr 2003 an erscheint die Zeitschrift *Zitteliana* in zwei Reihen.

Die *Reihe A: Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-412X) ersetzt die bisherigen „Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0077-2070). Die Bandzählung (zuletzt erschienen: Heft 43, 2003) wird fortgesetzt.

Die *Reihe B: Abhandlungen der Bayerischen Staatssammlung für Paläontologie und Geologie* (ISSN 1612-4138) führt die bisherige „Zitteliana – Abhandlungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie“ (ISSN 0373-9627) fort.

Hinweise für Autoren beider Reihen sind am Ende dieses Bandes enthalten.

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Bayerische Staatssammlung für Paläontologie und Geologie

Richard-Wagner-Str. 10, D-80333 München, Deutschland

<http://www.palaeo.de/zitteliana>

email: zitteliana@lrz.uni-muenchen.de

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Umschlagbild: *Phorcynis catulina* THIOLLIÈRE, 1854 (BSP 1990 XVIII 51) aus dem unteren Tithon von Zandt / Denkendorf (Bayern), Ventralansicht, 25 cm. Foto: G. JANßEN (LMU München, Department für Geo- und Umweltwissenschaften, Sektion Paläontologie)

Evolution of the Pachychilidae TROSCHEL, 1857 (Caenogastropoda, Cerithioidea) – from the Tethys to modern tropical rivers

By
Thorsten Kowalke*

Department für Geo- und Umweltwissenschaften, Sektion Paläontologie,
Richard-Wagner-Str. 10, D-80333 Munich, Germany

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Abstract

The evolutionary history and (palaeo-)ecology of the tropical brackish and freshwater gastropod family Pachychilidae TROSCHEL, 1857 is discussed. Eocene pachychilids inhabited the landward portions of coastal swamps, a generally euryhaline habitat. Pure fresh water habitats in fluvial or swamp palaeoenvironments were avoided. Investigation of the protoconch morphology of representatives from the European Eocene enables the reconstruction of the mode of early ontogenetic development. *Gantmelanatria* KOWALKE, 2001 is characterised by a free planktonic larval stage. Larvae of the lecithotrophic type spent a short time within the plankton where they fed on embryonic yolk. This mode of early ontogenetic development implies a fair connection of the adult habitat with the open sea. *Tinnyea* HANTKEN, 1887 from the European Oligocene to Late Miocene managed to colonize fresh water and preferred fluvial habitats. In contrast to modern pachychilids, *Tinnyea* tolerated warmer temperate conditions, as could be verified in *T. dactyloides* (SANDBERGER, 1885) from the Pannonian of Burgenland/Austria. Comparative investigation of the protoconch morphology of *T. dactyloides* and *T. lauraea* (MATHERÓN, 1843) from the Chattian of North Thrace/Turkey confirms the presence of different congeneric species of *Tinnyea*, characterising Upper Oligocene to Upper Miocene continental deposits. Both species lack a larval stage, and are characterised by a direct early ontogenetic development and protoconch morphology, which is similar to that seen in modern African fresh water dwellers of the genus *Potadoma* SWAINSON, 1840. In *Tinnyea* and *Potadoma*, brooding structures and the corresponding mode of lecithotrophic viviparity that occur in the South-east Asian genus *Brotia* H. ADAMS, 1866 are absent. The former taxa, along with the Neotropical *Pachychilus* I. & H. LEA, 1850 and *Melanatria* BOWDICH, 1822 from Madagascar, most probably form a separate clade within the Pachychilidae.

Key words: Pachychilidae, Tethys, tropics, ontogenetic strategies, (palaeo-)ecology, biogeography.

Zusammenfassung

Die Entwicklungsgeschichte und Paläoökologie tropischer Brack- und Süßwassergastropoden innerhalb der Pachychilidae TROSCHEL, 1857 wird diskutiert. Eozäne Pachychilidae charakterisierten die landwärtigen Bereiche von Küstensümpfen – generell euryhaline Habitate. Sie fehlten jedoch in fluvialen Biotopen und Süßwassersümpfen. Untersuchungen von Protoconchen von Vertretern aus dem europäischen Eozän ermöglichten eine Rekonstruktion des Modus der frühontogenetischen Entwicklung. *Gantmelanatria* KOWALKE, 2001 war durch eine freie planktonische Larvalphase gekennzeichnet. Lecithotrophe Larven verbrachten kurze Zeit im Plankton und ernährten sich von verbleibender embryonaler Dottersubstanz. Dieser Modus der frühontogenetischen Entwicklung setzte eine Verbindung des Adulthabitats mit dem offenen Meer voraus. *Tinnyea* HANTKEN, 1887 aus dem Europäischen Oligozän bis Späten Miozän besiedelte Süßwasser und bevorzugte fluviale Habitate. Im Gegensatz zu modernen Pachychilidae tolerierte *Tinnyea* warm gemäßigtes Klima, wie am Beispiel von *T. dactyloides* (SANDBERGER, 1885) aus dem Pannonium des Burgenlandes (Österreich) belegt werden konnte. Vergleichende Untersuchungen der Protoconche von *T. dactyloides* und *T. lauraea* (MATHERÓN, 1843) aus dem Chattium von Nordthracien (Türkei) bestätigten den Status verschiedener congenerischer Arten in kontinentalen Sedimenten im Zeitraum des Späten Oligozäns bis zum Späten Miozän. Beide Arten hatten keine marinen Larvalstadien, sondern waren durch eine direkte Entwicklung mit dem Schlupf kriechender Jungtiere gekennzeichnet. Hinsichtlich der frühontogenetischen Entwicklung und der korrespondierenden Protoconchmorphologie zeigen sie Ähnlichkeit zu afrikanischen Süßwassergastropoden der Gattung *Potadoma* SWAINSON, 1840. *Tinnyea* und *Potadoma* hatten keinen Brutbeutel und waren nicht durch einen entsprechenden Modus der lecithotrophen Viviparie wie die südostasiatische Gattung *Brotia* H. ADAMS, 1866 gekennzeichnet. *Tinnyea* und *Potadoma* bildeten offenbar mit der neotropischen Gattung *Pachychilus* I. & H. LEA, 1850 und *Melanatria* BOWDICH, 1822

*E-mail: t.kowalke@lrz.uni-muenchen.de

aus Madagaskar eine separate Abstammungsgemeinschaft innerhalb der Pachychilidae.

Schlüsselwörter: Pachychilidae, Tethys, Tropen, Ontogenese-strategien, (Paläo-)ökologie, Biogeographie

1. Introduction

The caenogastropod superfamily Cerithioidea exhibited a marked radiation of several intertidal families during the Late Cretaceous and Palaeogene, replacing the former primarily marine but euryhaline procerithiid dominated faunas (GRÜNDEL 1999, 2000; KOWALKE 1998a, 2002, 2003). Aside from the ubiquitous potamidids, which characterised the mud-flat and outer estuarine facies of the well structured marginal marine Tethys, Melanopsidae and Pachychilidae managed to colonize the landward portions of mangroves and large river estuaries. These habitats were formerly mainly settled by oligotypic assemblages of procerithiids, hydrobiids and archaeopulmonates (HUCKRIEDE 1967).

The inhabiting fauna of the extreme biotopes was adapted to considerable changes in salinity and a partly amphibious mode of life due to aerial exposure during low tides. In spite of the step by step migration into oligohaline coastal habitats, most Late Cretaceous/Early Cenozoic brackish water gastropods were unable to settle pure fresh water due to the prevailing indirect mode of early ontogenetic development. This ontogenetic strategy included a free planktonic larval stage, during which veliger larvae spent a more or less extended period in the plankton and fed on phyto-plankton or remaining embryonic yolk in case of lecithotrophic larval development respectively. When larvae reached convenient adult intertidal habitats, they underwent metamorphosis and passed into the benthic crawling mode of life. During the planktonic larval stage a characteristic larval shell was secreted, which is usually well separated from the subsequent adult shell. Thus, interpretation of the early ontogenetic palaeobiology of fossil gastropods, the interpretation of the mode of early ontogeny, and, in comparison, the resolving of systematic implications, is possible by investigations of the early ontogenetic shells (see KOWALKE 1998a and references therein).

The taxonomy and evolutionary history of Pachychilidae has largely been elusive and confusing for a long time, due to the lack of detailed investigations of the early ontogenetic shells of fossil and recent representatives and the lack of comparisons of anatomical data of the modern pan-tropical relatives. Early workers presented a very coarse classification of fresh water gastropods, summarising representatives of independent lineages under the family name Melaniidae LEACH, 1823, which represents a junior synonym of Thiaridae TROSCHEL, 1857. TROSCHEL (1856-1863) recognised the heterogeneity of the artificial group and subdivided the Melaniidae into tribes. The status of an independent family Pachychilidae, separated from the morphologically similar Melanopsidae, Paludomidae, Pleuroceridae, and Thiaridae, has later variously been confirmed. The taxonomic history of the Pachychilidae has been reviewed by KÖHLER & GLAUBRECHT (2002).

Extant Pachychilidae are restricted to the tropical realm (Fig. 1). Aside from the Oligocene to Miocene genus *Timmyea*,

standing warm temperate conditions during the Late Miocene, preceding Eocene and related modern taxa appeared to be strictly thermophile. Recent pan-tropical fresh water dwellers seem to prefer rapidly flowing rivers, but exhibit a certain ecological tolerance, occurring in smaller populations in calm portions of creeks, ponds, and in temporary biotopes such as flood plains (own observations).

This paper contributes to the understanding of the evolutionary history of the Pachychilidae by providing results of a comparative investigation of ontogenetic strategies and (palaeo-)ecology of fossil and modern representatives. The bio-geographical context is briefly discussed.

2. Material and Methods

Several hundred shells of all ontogenetic stages were collected from the Lutetian (Middle Eocene) of Gánt (West Hungary); for a detailed description of the locality and stratigraphic context of the section see BIGNOT et al. (1985). Oligocene material comes from the Chattian of Mimarşınan, North Thrace/Turkey. Extant material for comparison was collected from a second-order tributary of the Mungo River at Ediki and a flood plane of the Sanaga River at Edéa (both locations in SW Cameroon, West Africa).

Adult shells (teleoconchs) were cleaned and documented by macro-photography (Leica). The ecology and reproductive biology of extant gastropods was documented in the field. Spawn of extant gastropods was studied and documented by the aid of a photo-microscope (Leica DMLB). Juvenile specimens with preserved protoconchs were cleaned in an ultrasonic bath, sputter-coated with gold, and investigated and documented with a scanning electron microscope (SEM, Leitz AMR 1200). The dimensions of the early ontogenetic shells, i.e. the embryonic shell (protoconch I) and the larval shell (protoconch II) of fossil and extant gastropods were described. Protoconch I was analysed with regard to the width of the initial non-spiral cap-like onset of the embryonic shell and height and maximum diameter of the embryonic shell. Furthermore, the embryonic ornament and morphology of the transition to the larval shell, or to the teleoconch respectively, were analysed. In case of an additional larval development, the dimension and sculpture of the larval shell was described along with the morphology of the transition to the teleoconch.

The figured material is deposited in the collections of the Bayerische Staatssammlung für Paläontologie und Geologie (BSP 1980 X 170, BSP 1980 X 1187, BSP 2004 I 67 – BSP 2004 I 73) and of the Geologisch-Paläontologisches Museum Hamburg (GPIMH 4257, 4259).

3. Results

3.1 Origin of the Pachychilidae – the Eocene of the Tethys

Occurrences: The oldest known pachychilids are documented from the European Eocene: DOMINICI & KOWALKE (in prep.) recently discovered a large pachychilid from the Cuisian (Early Eocene) of the South Pyrenees. The protoconch is not

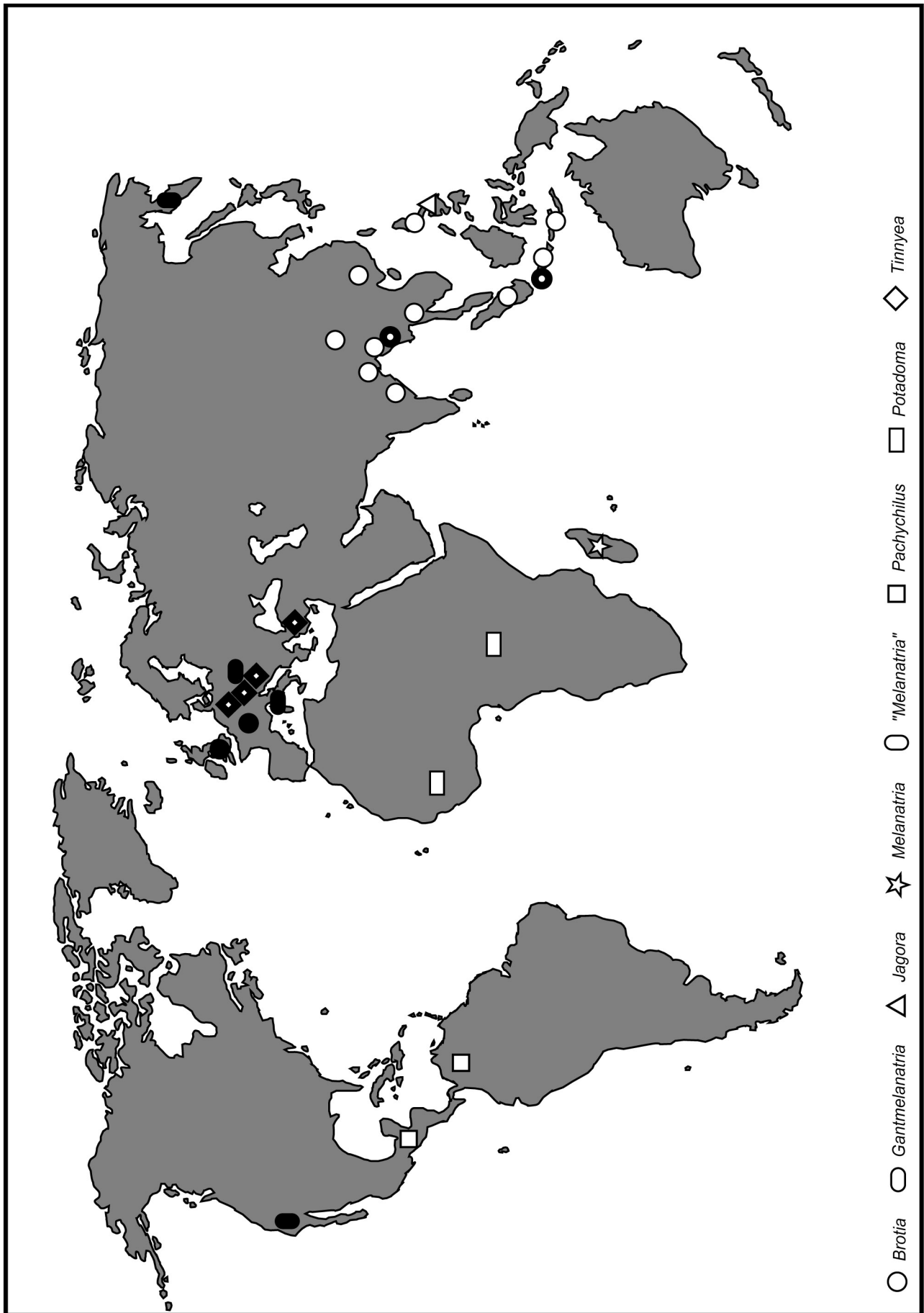


Figure 1: Distribution of fossil and recent representatives of the Pachychilidae TROSCHER, 1857. Filled symbols indicate Eocene occurrences, half-filled symbols = Oligocene and Neogene occurrences, white symbols = Extant occurrences

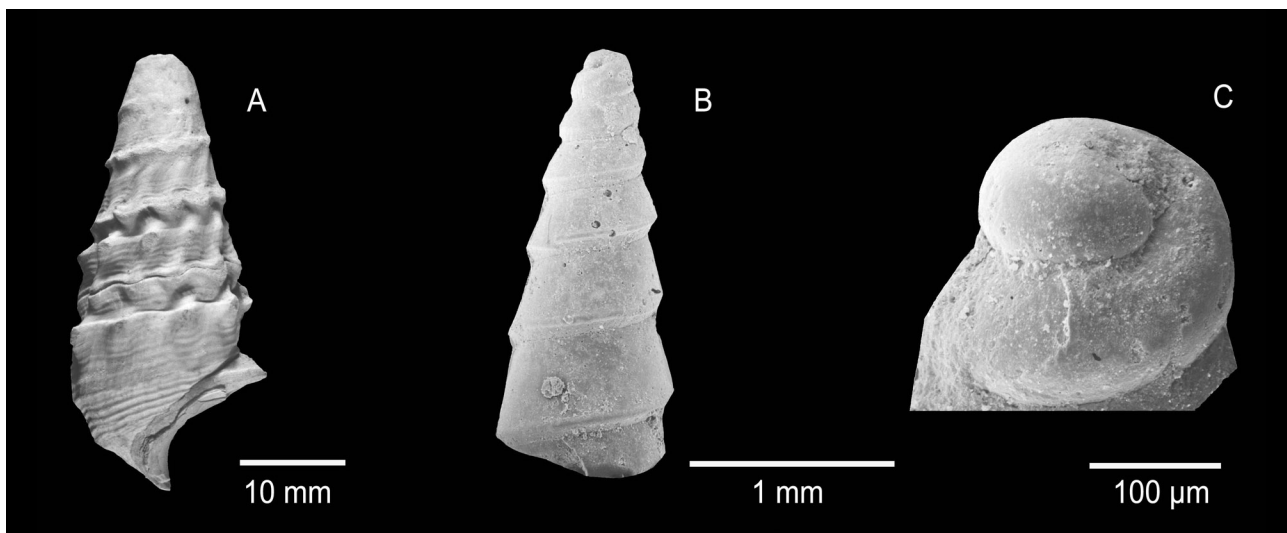


Figure 2: *Gantmelanatria auriculata* (SCHLOTHEIM, 1820). **A:** Adult specimen (GPIMH 4257) and **B-C:** juvenile specimen (GPIMH 4259), from the Lutetian of Gánt, West Hungary; showing the sculptural development during the ontogeny, with detailed view of the protoconch.

preserved. However, the early teleoconch morphology and sculptural details of late teleoconch whorls indicate a relation within the Pachychilidae (DOMINICI & KOWALKE in prep.). The similar genus *Gantmelanatria* KOWALKE, 2001, with its type species *Muricites auriculata* SCHLOTHEIM, 1820 (Fig. 2A-C), was widespread in the Middle Eocene of the Tethys. It has been reported from the Lutetian (Middle Eocene) of West Hungary (SZÖTS 1953; STRAUSS 1966; KECKSKEMÉTI-KÖRMENDY 1972; KOWALKE 2001), but is known to have occurred also in contemporaneous deposits of Italy (DE GREGORIO 1894; OPPENHEIM 1896). *Gantmelanatria* had tentatively been assigned to *Nodifaunus* Olsson, 1944, described from the Maastrichtian of Peru (OLSSON 1944) by KOWALKE (2001) on subgeneric level. Comparative analysis of the early teleoconch formation yielded significant differences that justify the generic status of *Gantmelanatria*, and more likely indicate a systematic placement of *Nodifaunus* within the family Cerithiidae. *Nodifaunus* most probably represents a precursor of the *Pseudovertagus*-relation (see KOWALKE 2002). Further Eocene fossils, e.g., from the Paris Basin (DESHAYES 1837), which are morphologically similar to the modern Southeast Asian genera *Brotia* H. ADAMS, 1866 and *Jagora* KÖHLER & GLAUBRECHT, 2003 (KÖHLER & GLAUBRECHT 2001, 2002, 2003), still need investigation, especially with regard to the morphology of the early ontogenetic shells.

“*Melanatria*” *markleyensis* (CLARK, 1938) has been documented from Upper Eocene deposits of South California. It has prominent nodes sculpturing the adapical portion of the teleoconch whorls (CLARK 1938; SQUIRES 1999). This species differs from modern *Melanatria* by the smaller, less slender shell with reduced axial sculpture, a higher last whorl, and a larger aperture. According to DEVYATILOVA & VOLOBUEVA (1981) and SQUIRES (1999), “*Melanatria*” *markleyensis* occurs also in Middle Eocene deposits of north-western Kamchatka.

Ontogenetic strategies: Due to the decollate status of adult shells and the frequent occurrences in coarse sediments the protoconch morphology of Eocene pachychilids was largely unknown to date. KOWALKE (2001) documented the protoconch of *Gantmelanatria auriculata* from the Lutetian of Gánt: The protoconch (Fig. 2C) has 1.4–1.6 rounded whorls

measuring 0.24–0.26 mm in height and in maximum diameter. The width of the initial cap amounts to 0.05 mm. The transition from protoconch to teleoconch is characterised by a sinuous rim, which is thickened in its adapical portion and thin and fragmented in its abapical portion.

The small size of the initial cap and the morphology of the transition to the teleoconch are indicative of a lecithotrophic larval development. The protoconch reflects a short larval stage, during which the larva was free-swimming in the plankton and feeding on remaining embryonic yolk. Larvae probably hatched in a late developmental stage, because embryonic and larval shell do not display demarcation by a thickened rim, which usually documents the moment of hatching (see KOWALKE 1998a). Compared to the corresponding extant mode of lecithotrophic development, larvae were most probably hatching as pediveligers, still characterised by a velum as a transitional organ, but able to settle at a convenient habitat, because the foot was already functional.

Palaeoecology: In Lutetian brackish water deposits of Gánt *Gantmelanatria* occurred as a rare element of coastal mangrove assemblages, predominantly characterised by Potamididae (*Tympanotonos*, *Cerithidea*), and in the mud-flat communities dominated by Pseudamauridae (KOWALKE 1998b, 2001). The pachychilid represented a more common faunal element of the calm coastal swamp facies, reflected by layers with very fine marl to clay sediment, rich in plant remains. The autochthonous character of the fauna is documented by the presence of all developmental stages in these layers, whereas the outer mangrove, mud-flat and outer estuarine section are characterised by scattered grown shells of *Gantmelanatria*. The preferred habitat of the Eocene *Gantmelanatria* is interpreted as a calm coastal swamp/lagoon facies. Fresh water habitats were avoided by *Gantmelanatria*. Typical fresh water habitats were settled by a well distinguished melanopsid-hydrobiid fauna. Obviously the mode of early ontogenetic development (see above) implies a fair connection of the adult habitat with the open sea to guarantee a sufficient reproduction by way of lecithotrophic veliger larvae, and excludes the settlement of pure fresh water palaeoenvironments. A very similar palaeoenvironment and

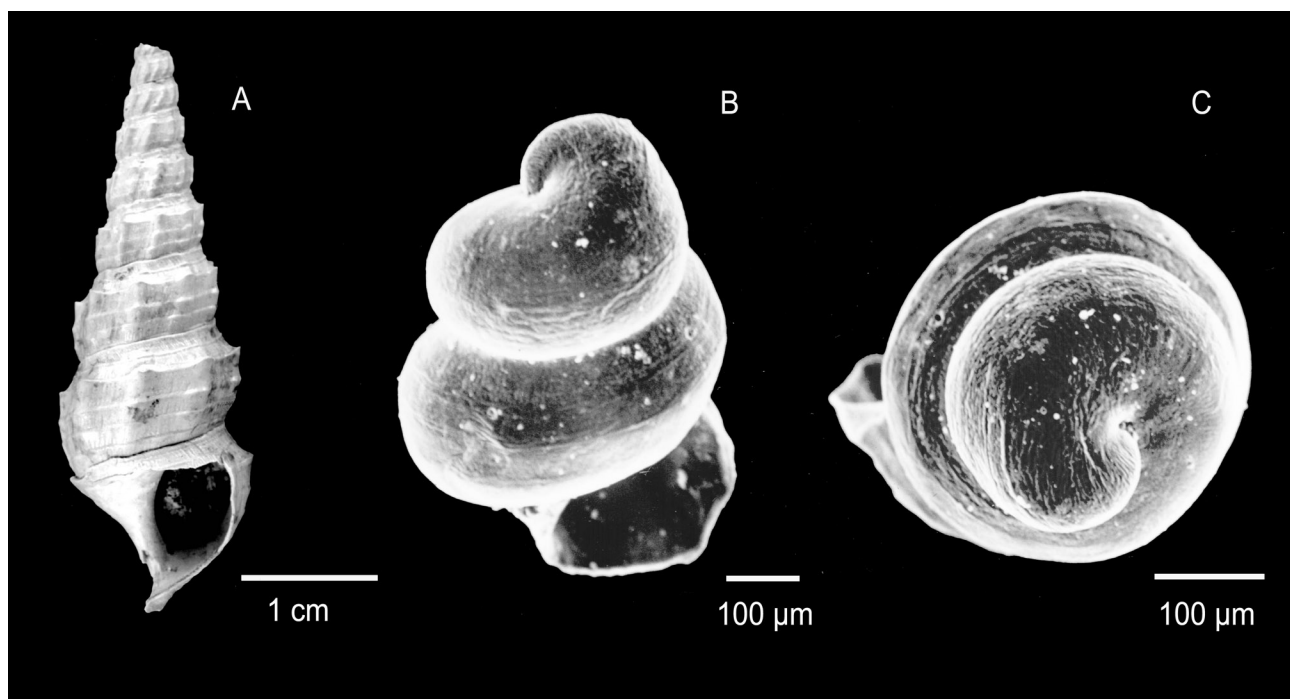


Figure 3: *Tinnyea lauraea* (MATHERÓN, 1843). **A:** Adult specimen (BSP 1980 X 170) from the Chattian of Edirköy, North Thrace/Turkey. **B-C:** Juvenile specimen (BSP 1980 X 1187) from the Chattian of Mimarsinan, North Thrace/Turkey; apertural and apical view, showing details of the protoconch.

corresponding habitat preference can be reconstructed for a pachychilid from the Cuisian (Early Eocene) of the South Pyrenees (DOMINICI & KOWALKE in prep.).

3.2 The Oligocene and Neogene Guild

Occurrences: Fossils from the European Oligocene and Miocene, mediating between the Eocene and modern pachychilids with regard to the morphology of the teleoconch, have been assigned to the modern genus *Brotia* by previous authors. The nomenclatorial context is confusing: The species complex has been summarised under “*escheri* BRONGNIART, 1822”, which represents a nomen nudum (CUVIER & BRONGNIART 1822, see also discussion and literature review in KADOLSKY 1995). The species name “*lauraea*” is the earliest valid name available. “*Brotia*” *lauraea* (MATHERÓN, 1843) occurred in the Late Oligocene of the Mainz Basin (KADOLSKY 1995), and the Late Oligocene to Early Miocene of France and of the eastern Mediterranean (NOULET 1846; RÜCKERT-ÜLKÜMEN 1990) and of the Central Paratethys (BALDI 1973; BINDER 2002). “*Melania*” *dactylodes* is reported from the Lower Pannonian of Leobersdorf, Austria (SANDBERGER 1885; HANDMANN 1887; HARZHAUSER et al. 2002). “*Brotia*” *vasarbelyii* (HANTKEN, 1887) occurs in Pannonian deposits of West Hungary (HÖRNES 1857; LÖRENTHEY 1902), of the Vienna Basin (PAPP 1953) and St. Margarethen, Burgenland, Austria (FISCHER 1994; HARZHAUSER et al. 2002). PAPP (1953) separated the Late Miocene species on subgeneric level (sg. *Tinnyea*). HARZHAUSER et al. (2002) separated the Pannonian species from *Brotia* based on comparisons of the protoconch morphology, and suggested a generic status of *Tinnyea* (see also section “ontogenetic strategies” below).

According to KÖHLER & GLAUBRECHT (2001), the fossil record of modern *Brotia* in South-east Asia extends back to the

Pliocene (and possibly Miocene?, dating of the sediments has been questioned). However, the generic affiliation of the fossils is questionable in detail since data concerning the protoconch morphology are unknown.

Ontogenetic strategies: *Tinnyea lauraea* (Fig. 3A-C) from the Chattian of Mimarsinan (North Thrace/Turkey) is characterised by a large protoconch comprising 2.25–2.4 bulbous whorls. It measures 0.6–0.62 mm in height and 0.46–0.47 mm in maximum diameter. The first whorl measures 0.32–0.33 mm in maximum diameter. The width of the initial cap amounts 0.16 mm. The initial 0.7 whorls are strongly folded. The subsequent part of the protoconch is more regularly mineralised. Six coarse folds and numerous additional fine spiral threads extend on the entire protoconch. The protoconch is terminated by a slightly thickened rim of the shell. The onset of the teleoconch is indicated by the formation of the regular adult sculpture of strong spiral keels and axial ribs.

Tinnyea dactylodes from the Pannonian of Lake Pannon has a similar protoconch with slightly smaller dimensions (Harzhauser et al. 2002: pl. 5, figs 1–3): It comprises two rounded whorls measuring 0.5 mm in height. The first whorl measures 0.3 mm in maximum diameter. The width of the initial cap amounts 0.1 mm. Ornament differs by the formation of ten spiral folds and numerous finer spirals intercalated.

The protoconch morphology of both representatives documents the presence of different species of the genus *Tinnyea* (species with similarly variable teleoconch morphology but characteristic consistent protoconchs). The protoconch morphology reflects a very yolk-rich embryogenesis resulting in similar early ontogenetic shells as described from modern *Potadoma* (see below).

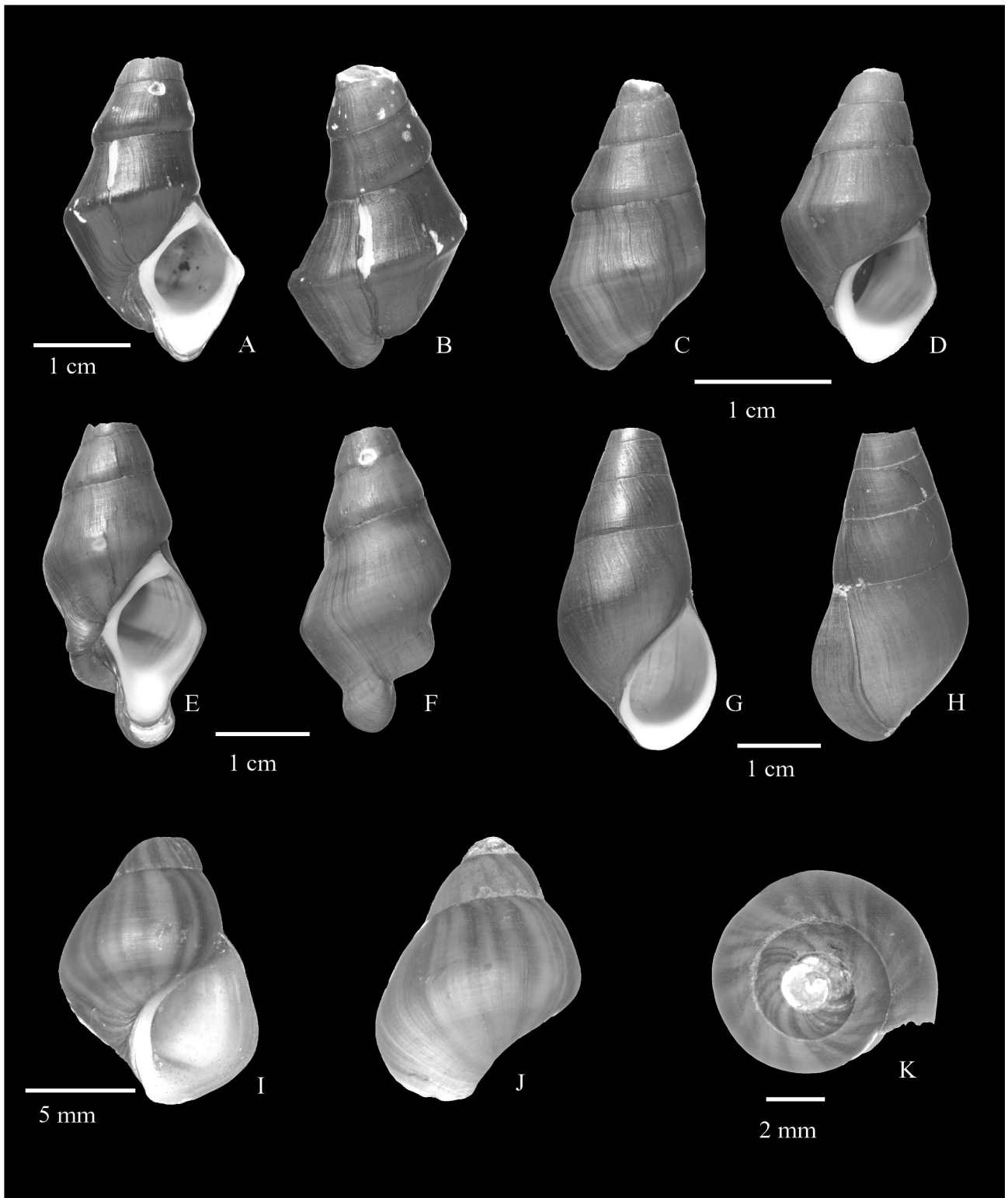


Figure 4: *Potadoma zenkeri* (MARTENS, 1901). **A-K:** Extant specimens (BSP 2004 I 67 - BSP 2004 I 71), from a flood plane of the Sanaga River at Edéa, Southwest Cameroon, showing the conchological variability and colour pattern.

Palaeoecology: *Tinnyea* preferred fresh water habitats, frequently present by monotypic mass occurrences. The Oligocene species *T. lauraea* from North Thrace occurred in very fine clays and marls indicating quiet water conditions. Shells of *T. dactylodes* from the Lower Pannonian of Leobersdorf have been extracted from marly limestone, which had been deposited in the context of hydrothermal waters. No indica-

tions for brackish water influx could be observed. Scattered occurrences in sandy sediments with intercalations of coarser pebbles reflect allochthonous transported shells in rapidly flowing rivers and creeks. The contemporaneous species *T. vasarhelyii* and the accompanying fauna, predominantly consisting of *Theodoxus* spp., obviously preferred more rapidly flowing rivers. However, both species are absent from the au-

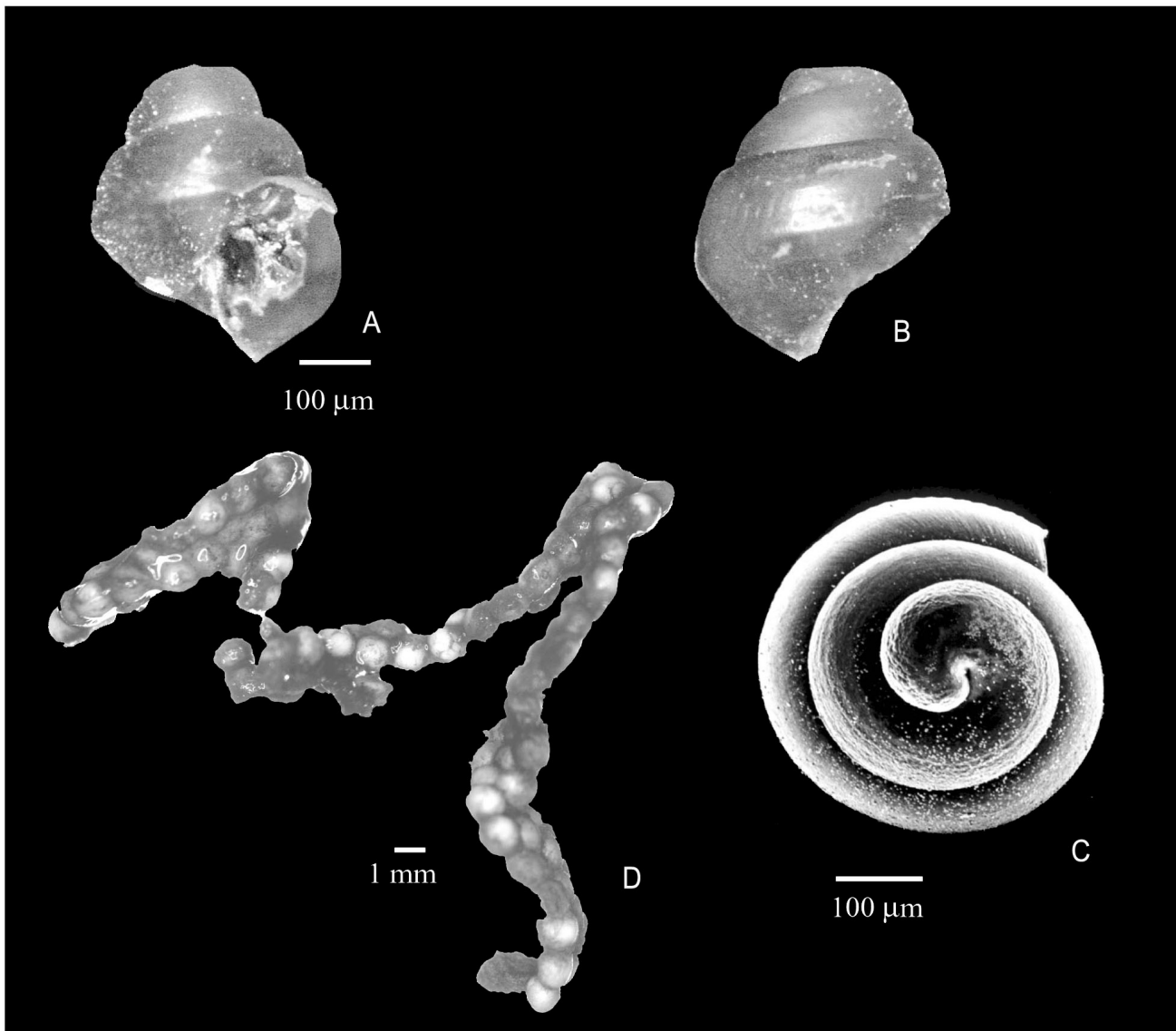


Figure 5: *Potadoma zenkeri* (MARTENS, 1901), extant, from a tributary of the Mungo River at Ediki, Southwest Cameroon. **A-B:** Juvenile specimen (BSP 2004 I 72), extracted from an egg-string, apertural and lateral view. **C:** Juvenile specimen (BSP 2004 I 73) extracted from an egg-string, apical view; SEM photo showing details of the protoconch. **D:** Spawn.

tochthonous brackish/oligohaline deposits of Lake Pannon (HARZHAUSER et al. 2002).

3.3 Extant Tropical Relations

Occurrences: Extant Pachychilidae show a pan-tropical distribution. They occur, well separated, in particular bioprovinces: *Pachychilus* I. & H. LEA, 1850 is distributed in the Neotropis. *Melanatria* BOWDICH, 1822 occurs in South-east Africa, restricted to Madagascar and Nossi Bé. The type species *Buccinum flumineum* GMELIN, 1767 settles rapidly flowing rivers of the primary forests (BROWN 1980). *Potadoma* SWAINSON, 1840 represents a Central and West African faunal element, which differs from *Melanatria* by the lack of any axial sculpture. The typical pachychilid spiral keel is more or less strongly developed and frequently vanishes in the course of the ontogeny, as could be observed in populations of *Potadoma zenkeri* (MARTENS, 1901) from Cameroon (Fig. 4A-K). The presence or absence of the keel does not depend on the habitat. Populations in rapidly flowing waters at Ediki exhibit

smooth specimens and others that display a strongly developed keel, connected by intermediate morphs. The same situation can be observed in quiet portions of a flood plane at Edéa. The number of specimens with and without keel is generally variable. Investigations on the protoconch morphology and radula anatomy did not yield differences, and thus indicate the presence of a single species *P. zenkeri*.

Extant *Brotia* and *Jagora* are characterised by a particular Southeast Asian occurrence (KÖHLER & GLAUBRECHT 2001, 2002, 2003). *Brotia* is distributed from Northeast India and South China to the Philippines and Indonesia. *Jagora* is restricted to the Philippines.

Ontogenetic strategies: The reproductive biology and early ontogenetic development of *Potadoma zenkeri* was studied in a second order tributary of the Mungo River near Ediki (Southwest Cameroon): Strings containing two rows of eggs (Fig. 5D), each measuring about one millimetre in diameter, are deposited in protected portions of the creek with reduced water energy. The spawn is preferably attached to rocks or

wood in shallow waters beneath the bank in less than 0.5 m depth. Young are hatching from the eggs with about 1.3 whorls completed. The protoconch measures 0.4–0.5 mm in maximum diameter. The width of the initial cap amounts 0.12–0.13 mm. The protoconch has a characteristic ornament: The initial half whorl is characterised by a wrinkled surface, reflecting retarded calcification of the shell, which later shrunk after hatching. The subsequent part of the protoconch has six closely spaced spiral folds and subordinated fine granulated spiral threads. The transition to the teleoconch is evident by the formation of regular closely spaced growth lines and a characteristic abapical spiral keel. Young were observed to move within the egg-strings, feeding on additional yolk until about three whorls of the shell are completed (Fig. 5A–C). The specimens proceed to the free benthic mode of life when the shells reached a height of 1–1.5 mm.

The extended, yolk rich embryogenesis and subsequent protected development within the egg-strings enables the release of individuals in an advanced developmental stage. This mode of early ontogenetic development appears advantageous especially in fluvial environments with high predation by juvenile fishes.

An oviparous mode of early ontogenetic development also is present in the extant pachychilids *Melanatria* and *Pachychilus* (KÖHLER & GLAUBRECHT 2003); however, the protoconch morphology of representatives from these genera is unknown.

A different ontogenetic strategy has been reported by KÖHLER & GLAUBRECHT (2001, 2002, 2003) for species of the South-east Asian genera *Brotia* and *Jagora*. In case of *Brotia* the early ontogenetic development takes place within a brood pouch, whereas in *Jagora* eggs are retained within the mantle cavity. Development in both cases differs from the histotrophic strategy, present in viviparous Thiaridae, by the absence of secretory epithelia and adelphophagy. Thus, nourishment is restricted to the large amount of yolk/albumen, resulting in a strongly retarded calcification of the early ontogenetic shells.

Ecology: Extant pachychilids prefer rapidly flowing rivers of the tropics where they need fair oxygen content of the water. To a lesser degree, smaller populations established in protected portions, including flood planes. However, these habitats are well connected to the main rivers. Specimens quickly die when they are kept in boxes under quiet water conditions (own observations on *Potadoma* from Cameroon).

Extant pachychilids apparently do not display habitat preferences with regard to micro-habitat. They occur on hard substrates, e.g., living attached to rocks and wood, as well as on sandy substrates. In case of the settlement of more calm portions of rivers and creeks, they occur on and buried in muddy substrate and under leaves (see also KÖHLER & GLAUBRECHT 2001 and references therein). DAVIS (1982) documented an eco-phenotypical dimorphism in the extant *Brotia costula* (RAFINESQUE, 1833) from Malaysia, with costulate morphs characterising quiet portions of the rivers, and spiny morphs being present in rapidly flowing water.

4. Discussion and Conclusions

Early pachychilids were widespread in the marginal marine

facies of the Early Cenozoic. Representatives are known from the Eocene of North America (SQUIRES 1999) and Kamchatka (DEVYATILOVA & VOLOBUEVA 1981) and of Europe (DE GREGORIO 1894; OPPENHEIM 1896; SZÖTS 1953; STRAUSS 1966; KECKSKEMÉTI-KÖRMENDY 1972; KOWALKE 2001; DOMINICI & KOWALKE in prep.). The Lutetian *Gantmelanatria* characterised the landward portions of coastal swamps, but represented a rare faunal element of the outer estuarine sections and seaward mud-flats, which were dominated by potamidids and pseudamurids. *Gantmelanatria auriculata* had a planktonic larva, a lecithotrophic short time veliger, which was free swimming in the plankton and feeding on remaining embryonic yolk. This mode of early ontogenetic development implies a fair connection of the adult habitat with the open sea, and consequently *G. auriculata* was absent in pure fresh water habitats.

The genus *Tinnyea* occurs in Oligocene to Upper Miocene deposits of the Mainz Basin, of the Mediterranean and of the Central Paratethys (SANDBERGER 1885; HANDMANN 1887; BALDI 1973; RÜCKERT-ÜLKÜMEN 1990; FISCHER 1994; KADOLSKY 1995; BINDER 2002; HARZHAUSER et al. 2002). *Tinnyea* inhabited fresh water palaeoenvironments, and in contrast to modern pachychilids, preferred quiet water conditions and less rapidly flowing rivers. In contrast to the Eocene *Gantmelanatria*, *Tinnyea* did not tolerate brackish water conditions: *T. dactylodes* and *T. vasarhelyii* from the Pannonian of Austria settled adjacent fresh water habitats, but are absent in the brackish/oligohaline layers of Lake Pannon (HARZHAUSER et al. 2002). *Tinnyea* spp. lack a larval stage, and are characterised by a direct yolk-rich early ontogenetic development and corresponding protoconch morphology. Comparative analyses of the protoconch morphology confirm the presence of different species of the *Tinnyea*-complex in Oligocene to Upper Miocene continental deposits of the Mediterranean and of the Paratethys.

Comparative analyses of the protoconch morphology of *Tinnyea lauraea* from the Chattian of Turkey and of *T. dactylodes* from the Late Miocene of Austria with the modern African fresh water dweller *Potadoma zenkeri* from Cameroon indicate the presence of very similar early ontogenetic shells, and suggest a very similar mode of early ontogenetic development. Modern *Potadoma* is characterised by a very yolk-rich embryogenesis. Several hundred eggs, each measuring about one millimetre in diameter, are arranged in egg-strings. After hatching, the juveniles are supported by further yolk nourishment, moving within the egg-strings and feeding on additional yolk until they reach a size of more than one millimetre in height, comprising about three whorls of the shell completed. A similar yolk-rich embryogenesis occurred in *Tinnyea*, as can be interpreted based on the corresponding morphology of the embryonic shell.

Tinnyea and *Potadoma* lack brooding structures like those seen in the South-east Asian genus *Brotia*, and most probably, along with *Pachychilus* and *Melanatria*, formed a separate clade within the pachychilid relation. *Melanatria*, *Potadoma*, and *Pachychilus* obviously represent the more “ancient guild” within the modern Pachychilidae, which derived from *Tinnyea* and relatives. *Tinnyea* had evolved from the Tethyan *Gantmelanatria*-relation during the Palaeogene. Along with the pre-adaptational loss of planktonic larval development, the colonization of fresh water palaeoenvironments was possible. The early adaptation to fluvial habitats and the thermophile character

of modern pachychilids, preferring tropical climates, restricted the far distribution of taxa after disintegration of the Tethys. *Brotia* and *Jagora* represent the most modern pachychilid taxa. The split distribution of these, and probably additional yet undiscovered taxa in South-east Asia correlates with the complex geological history of the region (see discussion in KÖHLER & GLAUBRECHT 2001). Environmental changes in addition to syn-ecological features obviously pushed the evolutionary development, with the achievement of secondary anatomical structures and modes of early ontogenetic development, e.g., the development of a brood pouch in *Brotia* and corresponding changes in the embryogenesis. The very stable conditions that characterise the African and Neotropical fresh water environments resulted in the formation of very conservative lineages of *Pachychilus* in South and Middle America, *Melanatria* in Madagascar, and *Potadoma* in West Africa, which modes of life-cycles have not significantly changed, compared to that of the preceding relatives, since the Late Palaeogene.

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