GEOLOGICA SAXONICA
Journal of Central European Geology

61 (1): 35–51
2 Jan 2015

SENCKENBERG

Lutetiella, a new genus of hydrobioids from the Middle Eocene (Lutetian) of the Upper Rhine Graben and Paris Basin (Mollusca: Gastropoda: Rissooidea s. lat.)

Lutetiella, ein neues Genus von Hydrobioiden aus dem Mitteleozän (Lutetium) des Oberrheingrabens und Pariser Beckens (Mollusca: Gastropoda: Rissooidea s. lat.)

Dietrich Kadolsky

66 Heathhurst Road, Sanderstead, Surrey CR2 0BA, United Kingdom; kadolsky@btsgeo.com

Revision accepted 17 November 2014.
Published online at www.senckenberg.de/geologica-saxonica on 1 December 2014.

Abstract

Lutetiella n.gen. is proposed for *Lutetiella hartkopfi* n. sp. (type species) and *L. conica* (Prévost 1821) from the Middle Eocene (Lutetian) of the Upper Rhine Graben and Paris Basin, respectively. The protoconch microsculpture of *L. hartkopfi* n. sp. was occasionally preserved and proved to be a variant of the plesiomorphic hydrobioid pattern. The new genus is tentatively placed in Hydrobiidae. Problems in the classification of hydrobioid fossils are discussed, arising from the dearth of distinguishing shell characters. Previous attributions of *L. conica* to *Assiminea* or *Peringia* are shown to be incorrect. The name *Paludina conica* Férussac 1814, a senior primary homonym of *Paludina conica* Prévost 1821, and denoting an unidentifiable hydrobioid, threatens the validity of the name *Lutetiella conica* (Prévost 1821) and should be suppressed. Both *Lutetiella* species are interpreted to undergo a planktic veliger larval stadium and lived in shallow brackish waters. The species difference may be due to geographical isolation between the Paris Basin and the Upper Rhine Graben.

Kurzfassung

Für *Lutetiella hartkopfi* n.sp. (Typusart) und *L. conica* (Prévost 1821) aus dem Mitteleozän (Lutetium) des Oberrheingrabens bzw. des Pariser Beckens wird ein neues Genus *Lutetiella* vorgeschlagen. Die manchmal erhaltene Protokonchmikroskulptur von *L. hartkopfi* n.sp. erwies sich als eine Variante des plesiomorphen hydrobioiden Grundtyps. Das neue Genus wird vorläufig in die Familie Hydrobiidae gestellt. Probleme der Klassifikation fossiler Hydrobioiden, die durch die Knappheit an erkennbaren Gehäusemerkmalen bedingt sind, werden diskutiert. Frühere Zuordnungen der *L. conica* zu *Assiminea* oder *Peringia* werden als inkorrekt erkannt. Der Name *Paludina conica* Férussac 1814, ein älteres primäres Homonym von *Lutetiella conica* (Prévost 1821), bezeichnet eine nicht identifizierbare Hydrobioide und sollte unterdrückt werden, da er die Validität des Namens *Lutetiella conica* (Prévost 1821) gefährdet, Bei beiden *Lutetiella*- Arten wird planktisches Veligerlarvenstadium und brackische Flachwasserbiotope angenommen. Die Artdifferenzierung dürfte durch geographische Isolation zwischen dem Pariser Becken und dem Oberrheingraben bedingt sein.

Introduction

The informal term “hydrobioids”, coined by Davis (1979), refers to gastropods which would traditionally have been classified in the family Hydrobiidae. Neozoological reassessments of the taxonomy and phylogeny of this group during the last five decades, initially based on anatomy, and then increasingly on molecular genetics, have resulted in a division of the traditional “Hydrobiidae” into numerous families, e. g.: Hydrobiidae Stimpson

ISBN 978-3-91000654-6 | ISSN 1617-8467

1865 s. str., Tateidae Thiele 1925, Cochliopidae Tryon 1866, Pomatiopsidae Stimpson 1865, Amnicolidae Tryon 1863, Lithoglyphidae Tryon 1866, Emmericiidae Brusina 1870, Bythinellidae Locard 1893, Moitessieriidae Bourguignat 1863, and others. Several of them are further subdivided into subfamilies (Davis 1979, Wilke et al. 2000, Wilke et al. 2001, Liu et al. 2001, Bouchet & Rocroi 2005, Szarowska 2007, Wilke et al. 2012, Crispione & Ponder 2013). More changes at the suprageneric level can be expected when more taxa will be so investigated. The hydrobioids are traditionally included in the superfamily Rissooidea Gray 1847, which Crispione & Ponder (2013) propose to divide in two superfamilies; in this case the hydrobioids would belong to the Truncatelloidea Gray 1840.

Unfortunately, the traits distinguishing the hydrobioid families are often not expressed in shell characters. In particular, the families Hydrobiidae, Pomatiopsidae, Tateidae and Cochliopidae cannot consistently be identified by shell characters (Hershler & Ponder 1998; author's observations). Consequently, reliable familial assignments of fossils are in many cases impossible and in even more cases uncertain. The phylogenetic relationships of many fossil taxa remain therefore uncertain.

The fundamental problems arising in the classification of fossil hydrobioids were discussed, i. a., by Kadolsky (2008b: 232–233). Despite the near-impossibility of arriving at a reliable phylogenetic classification at the genus and family level, at the species level many taxa can be differentiated from other taxa by their shell characters. Such „conchological species" may or may not represent biological species which can neither be proven nor disproved in these fossils. In some cases species groups can be recognized by shared shell characters. If their spatial and temporary distribution also supports the probability of a shared common ancestor, such species groups may be treated as genera. In this study one such group of species is revised and a new genus *Lutetiella* is proposed for them.

Material and methods

Shells were examined from historical collections as well as from recent temporary outcrops. Shell dimensions were measured and shells were drawn with a Wild M5 binocular microscope. For the taxonomic assessment, many specimens of *Lutetiella hartkopfi* n.gen. n. sp. were investigated by SEM to illustrate protoconch and teleoconch microsculpture. Initial results were discouraging particularly for the protoconch, showing shell corrosion and striations caused by differential movement of claystone matrix. Eventually, juveniles recovered from the interior of adult shells showed sometimes the original protoconch microsculpture. For *Lutetiella hartkopfi*, one out of 17 specimens so investigated had the protoconch microsculpture well preserved, and 5 more showed vestiges of it. In four investigated specimens of *Lutetiella conica* the protoconch was corroded, so that even the boundary to the teleoconch was not recognizable with certainty.

Voucher and reference material is located in the Senckenberg Forschungsinstitut und Naturmuseum Frankfurt (SMF), the Natural History Museum London (NHMUK), the Muséum National d'Histoire Naturelle, Paris (MNHNP), the Dipartimento di Scienze Ambientali, Università degli Studi di Siena, Italy and in the collections of Jacques Le Renard (Paris) and the author.

Taxonomy

Clade: Caenogastropoda Cox 1960

Clade: Hypsogastropoda Ponder & Lindberg 1997

Subclade: Littorinimorpha Pchelintsev 1963

Superfamily: Rissooidea Gray 1847 s. lat. (Truncatelloidea Gray 1840 sensu Crispione & Ponder 2013)

Family: ?Hydrobiidae Stimpson 1865

***Lutetiella* n. gen.**

Type species: *Lutetiella hartkopfi* n. sp.

Diagnosis: A hydrobioid genus with an ovate-conical shell reaching more than 7 whorls and more than 8 mm height; in the type species, the protoconch 1 has 0.4–0.6 convex whorls with a microsculpture of densely spaced, short, connected wrinkles without a preferred orientation; these wrinkles are strongest on the nucleus, decreasing on its later growth stages; a protoconch 2 is present, but sometimes not clearly distinguishable from the teleoconch; it ends at 1,25–1,75 whorls; its sculpture consists of growth lines and broad, rounded spiral ribs, both of which can be very weakly developed to absent, or strong. Teleoconch always with growth lines and fine, densely spaced spiral striae. First whorl nearly planispiral, the following descending rapidly, weakly to distinctly convex, rounded or with a blunt peripheral angle and a narrow and indistinct adapical ramp; sutures slightly appressed or deepened; last half whorl not or very weakly contracting and rarely stronly 'pulled in', but aperture contracts adapically; teleoconch sculpture of distant collabral growth lines with 2–5 smaller growth lines in the intervals; direction of growth lines on middle whorls slightly prosocline, near the adult aperture becoming opisthocyrt; apertural margin abapically protracted; aperture pear-shaped, slightly protracted adapically, with well developed parietal callus; columellar edge long and straight, joining the parietal margin at an

angle or in a continuous arc; palatal margin not thickened, shell wall tapering towards palatal edge, inner shell layer often terminating before having reached the palatal margin; no lip or terminal varix; umbilicus narrow or closed, a pseudumbilicus is often formed by the raised columellar margin.

Derivatio nominis: 'La petite Parisienne', from lat. Lutetia (= Paris), alluding to the occurrence of *L. conica* (Prévost 1821) in the Lutetian (Middle Eocene) of the Paris Basin, and the occurrence of *L. hartkopfi* n. sp. in the Lutetian of the Upper Rhine Graben.

Included species: *L. hartkopfi* n. sp. from Lutetian strata in the Upper Rhine Graben; *Paludina conica* Prévost 1821 from Lutetian strata of the Paris Basin. In Eocene and Palaeocene formations of the Paris Basin several other relatively large conical hydrobioid species occur which may be congeneric, but require further study: *contracta* Cossmann 1888 [*Assiminea* (*Assiminea*)], *crassa* Deshayes 1862 [*Bithinia*], *distinguenda* Cossmann 1899 [*Assiminea*], *glandinensis* Laubrière & Carez 1881 [*Bithinia*], and possibly *goniophora* Morlet 1888 [*Bithinia*].

Relationships: *Wallaua* R. Janssen 2007 with the only included species *W. flexiplicata* R. Janssen 2007 from the Early Oligocene Pechelbronn Formation of the Upper Rhine Graben is similar by its elongate-ovate shape and the first protoconch whorl being nearly planispiral, but differs by the presence of distinct and regular collabral ribbing, small size resulting from a lesser number of whorls and a larger protoconch not showing a differentiation into protoconch 1 and 2. Details of the differences are compiled in Table 1. The two species included in *Lutetiella* differ collectively from *Wallaua flexiplicata* by: their relatively small protoconch nucleus (75–100 µm diameter); on the teleoconch the presence of growth lines instead of ribs, and dense regular spirals. At the same number of whorls shells of *Wallaua flexiplicata* have dimensions and proportions similar to those of *Lutetiella hartkopfi*, but are less conical in outline. *Wallaua flexiplicata* achieves 3.1 mm height at 5.2 whorls, while *Lutetiella* species achieve heights up to 8.6 mm by adding up to 2.0 more whorls.

The placement in *Assiminea* suggested by Sandberger (1870–72) and Cossmann (1888) is certainly incorrect. The protoconch microsculpture in *Assiminea* is dominated by spiral elements (Kowalke 1998, Fukuda & Ponder 2006, Janssen 2007, van Aartsen 2008) which are absent in *Lutetiella hartkopfi* n. sp., the only *Lutetiella* species whose protoconch microsculpture is known.

Cossmann (1913) placed *Lutetiella conica* in the recent genus *Peringia* Paladilhe 1874 (Hydrobiidae: Hydrobiinae), which was accepted by all subsequent authors. The modern type species, *P. ulvae* (Pennant 1777), has a planktic veliger stage. The sculpture and dimensions of the protoconch shell was described by Bandel (1975) and Fish & Fish (1977). Their data refer to the unmineralized shell of the larva which becomes mineralized only when the teleoconch is formed. It consists of a small protoconch 1 of 0.5 whorls and 185 µm diameter which is covered with connected tubercles forming a pitted or granulose surface. The boundaries between protoconch 1 and 2, and between protoconch 2 and the teleoconch are abrupt. The sculpture of protoconch 2 consists of 14–17 raised spiral threads separated by wide flat spaces. How these patterns are expressed after mineralisation is poorly known as the shells are usually corroded. The author observed in one specimen spiral furrows in the place of the spiral threads of the larval protoconch 2. In *Lutetiella hartkopfi* the protoconch 1 is slightly smaller than in *Peringia ulvae*; it has a similar number of whorls, but it is covered with connected wrinkles which are isometric and strong on the nucleus; on protoconch 2 they are weak and superimposed by broad and rounded spiral ribs and growth lines. The boundary between protoconch 2 and teleoconch is sometimes indistinct. The dimensions of protoconch 1 in conjunction with the presence of a protoconch 2 in *Lutetiella hartkopfi* suggest that this species a planktic veliger larval stade. The same is likely in *Lutetiella conica,* too, although the state of preservation of the early whorls precludes a reliable assessment.

The similarities in the early development stages of *Peringia* and *Lutetiella* are interpreted as plesiomorphics: the protoconch dimensions are similar to those of many other hydrobiids; a protoconch 1 microsculpture of connected tubercles or wrinkles is common to all Hydrobiidae and many Cochliopidae and Pomatiopsidae. And, obviously, growth lines and spiral ribs are common sculpture elements in most gastropods with a shell. The spiral threads of the protoconch 2 of *Peringia ulvae*, however, constitute an apomorphic character state of *Peringia*.

There is no continuous fossil record of taxa potentially assignable to *Peringia* from the present to the Eocene. Wenz (1926: 1978–1987) lists a cluster of „*Peringia*" species in the Palaeocene and Eocene (of which at least „*Peringia*" *conica* belongs to *Lutetiella*), one species in the Early Oligocene and three questionable species in the Miocene. Of the latter, „*Assiminea*" *conoidea* Koenen 1882 was placed in the synonymy of *Odostomia conoidea* (Brocchi 1814) by Anderson (1964: 323). „*Assiminea" gottscheana* Koenen 1882 was placed in *Putilla* (*Ovirissoa*) by Anderson (1960: 19–20); while this genus and subgenus assignment need revision, a placement in the *Setia* group of the Rissoidae or in *Eatonina* (family Cingulopsidae) is conceivable. The third Miocene species, „*Paludestrina*" *rocae* Pallary 1901 (:165, pl.3 f.31) from of Algeria, has not been taxonomically revised; it has a strongly opisthocline peristome, unlike *Peringia* (or, for that matter, *Lutetiella* or *Mercuria*) and may not belong to any of them. The Plio-Pleistocene taxa listed by Wenz (1926), which include material identified as *Peringia ulvae*, need revision, too; but it is possible that at least some may indeed belong to *Peringia*. Thus, there is a time gap in the fossil record between possible *Peringia* species in the Plio-Pleistocene, and *Lutetiella* in the Eocene, or possibly Early Oligocene to Palaeocene.

Mercuria Boeters 1971 (Hydrobiidae: Nymphophilinae) is similar in size and shape, but differs by its larger protoconch 1 with 1.0 – 1.2 whorls and absence of protoconch 2 indicating direct development, and with a microsculpture of small isometric pits and tubercles (not confluent wrinkles). The teleoconch whorls in *Mercuria* are more convex, resulting in a stepped shell outline, and the aperture is often less strongly appressed to the preceding whorl. The shells of *Mercuria* species cannot on the genus level be distinguished from shells of species of *Pseudamnicola* Paulucci 1878 (Hydrobiidae: Pseudamnicolinae). As a consequence, *Mercuria* is reliably identified only since the Pleistocene. A number of Miocene and Oligocene hydrobioids could be placed either in *Mercuria* or *Pseudamnicola*, or possibly in additional genera with convergent shell characters; they differ consistently from *Lutetiella* by their smaller size and larger protoconch (pers.obs.).

The true phylogenetic relationships of *Lutetiella* remain at present unresolved. Even the assignment to the Hydrobiidae remains uncertain, let alone a subfamily assignment. There are no consistent shell characters to distinguish recent members of the families Hydrobiidae and Cochliopidae (Hershler & Ponder 1998), and this statement can be extended to the Pomatiopsidae and Tateidae. Similar protoconch microsculpture exists in all four families. Planktic veliger stades are known in the Hydrobiidae from *Peringia ulvae* only, and in the Cochliopidae in the subfamilies Semisalsinae, genera *Heleobia* and *Texadina*, and in the subfamily Littoridininae, genera *Littoridinops*, *Onobops* and *Spurwinkia* (Marcus & Marcus 1963, Hershler & Thompson 1992). The Hydrobiidae s. str. have their centre of distribution in the temperate to subtropical region of the entire northern hemisphere. The Tateidae occur in Australia and adjacent islands. The focus of the Pomatiopsidae is in tropical Asia, with few genera known from Africa, Australia and tropical South America; the focus of modern Cochliopidae is in tropical and subtropical America, with minor extensions into tropical Africa and subtropical to temperate Europe and North Africa (Hershler & Thompson 1992). However, a familial assignment of fossils on geographical grounds is tentative at best, and may lead to circular biogeographical and taxonomic reasoning. The discovery of modern to Pliocene Cochliopidae in the Palaearctic region (genus *Heleobia* Stimpson 1865; see Davis et al. 1982, Giusti & Pezzoli 1984, Bank & Butot 1984, Schütt 1988) and the assignment of the genus *Bouryia* Cossmann 1888 from the Lutetian of the Paris Basin to Pomatiopsidae (based on the synonymy, as proposed by Le Renard (1997), with the modern *Floridiscrobs* Pilsbry & McGinty 1949 from Florida, assigned to Pomatiopsidae by Fukuda & Ponder (2003)) suggests that representatives of these families had reached Europe by natural means in the past.

In this situation it is proposed to assign all fossil Palaearctic hydrobioid taxa with a tuberculate or pitted microsculpture of the protoconch questionably to Hydrobiidae, unless specific reasons suggest a relationship with the Cochliopidae or Pomatiopsidae. An example of this procedure is the description of a hydrobioid from a Late Oligocene lake deposit in the Rhön Mountains, Germany, as *Heleobia* (*Eupaludestrina*) *rhoenana* by Kadolsky (2008a). Although the general shell shape and plesiomorphic protoconch microsculpture would have allowed assignment to *Hydrobia* (s.lat.), the great shell similarity to the modern *Heleobia* (*Eupaludestrina*) *macei* (Paladilhe) from the Mediterranean area and a freshwater habitat (as has *Heleobia macei*, but not *Hydrobia* s.lat.) were taken as reason for a classification in *Heleobia*.

***Lutetiella hartkopfi* n. sp.**
Figs. 1 – 9, Tab. 1

Holotype: SMF 341586, here Fig. 1.

Locus typicus: Temporary exposure at the road B10 between Birkweiler and Albersweiler, Rhineland-Palatinate, Germany. Gauss-Krüger coordinates: R ^{34}29730, H ^{54}52950, Map sheet 1 : 25.000 no. 6714 Edenkoben.

Stratum typicum: Landauer Mergel, Eocene, early to middle Lutetian[1].

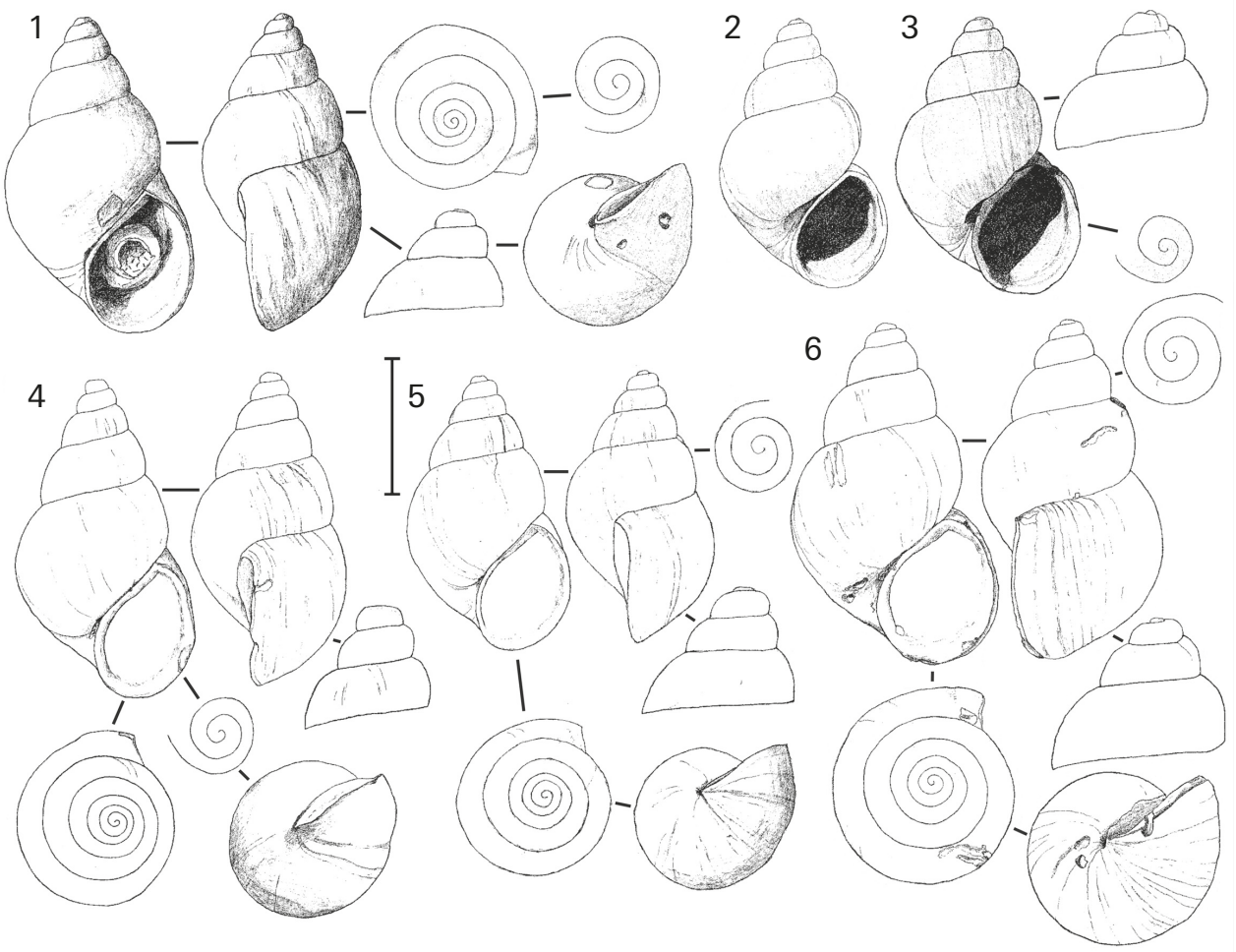
Paratypes: Numerous shells from the type locality, and from an adjacent borehole (R ^{34}29675, H ^{54}52968), depth 27.8 – 28.0 m (+ 171.2 – 171.0 m NN), SMF 341587 – 341589, 341599, 341600, 341603 and SEM preparations (SMF 344883 – 344884). A few shells in coll. Giusti (Siena) and coll. Kadolsky.

Derivation nominis. In recognition of Dr. Christopher Hartkopf-Fröder (Krefeld), who provided most of the material and who undertook most of the SEM work.

Preservation: Shell surfaces slightly corroded, with scratchmarks from sediment movement, some shells with impressions of sand grains; shells usually broken, mostly chalky-white, sometimes brown and black; infill is greenish claystone, muddy very fine sand or sparry calcite.

Diagnosis: *Lutetiella hartkopfi* differs from *L. conica* by its dimensions: at any given number of whorls *L. hart-*

[1] The outcropping strata are (abbreviated reference: Birkweiler) dated as early to middle Lutetian (Middle Eocene) through its nannoplankton (Martini, in prep.) and palynoflora (Hartkopf-Fröder & Hottenrott, in prep.). Another outcrop in the vicinity yielded charophytes indicating the *Maedleriella embergeri* charophyte zone (Schwarz & Griessemer 1998), similarly indicative of the Early to Middle Lutetian. Breuer & Feist (1986) reported an association of foraminifera with charophytes of the *Maedleriella embergeri* charophyte zone from a well in the Landau Oil Field, not far from Albersweiler, and named the interval „Landauer Mergel“ [Landau Marl]. This informal lithostratigraphic term is here extended to the brackish claystones and sandstones of the Albersweiler outcrop. A comprehensive review of the biostratigraphic position of the Albersweiler biota is in preparation (Hartkopf-Fröder et al.).



Figs. 1–6. *Lutetiella hartkopfi* n. sp. Temporary exposure at the road B10 between Birkweiler and Albersweiler, Rhineland-Palatinate, Germany. Eocene, Lutetian, Landauer Mergel. Scale represents 2 mm for all views of entire shells, and 1 mm for the partial views showing the early whorls only.

Fig. 1. Holotype (SMF 341586). Shell with large and slightly 'pulled-in' last whorl; whorls moderately convex.
Fig. 2. Paratype (SMF 341588). Smaller and slender shell with relatively small aperture; parietal wall loosely attached to shell wall, creating a relatively large pseudumbilicus; whorls more distinctly convex.
Fig. 3. Paratype (SMF 341589). Shell with large last whorl and distinctly convex whorls.
Fig. 4. Paratype (SMF 341590). Slender shell with relatively small last whorl, hardly 'pulled-in', whorl outline modestly convex.
Fig. 5. Paratype (SMF 341591). Broader shell with large last whorl, hardly 'pulled-in', whorl outline modestly convex.
Fig. 6. Paratype (SMF 341587). Slender shell with relatively small last whorl, hardly 'pulled-in', whorl outline distinctly convex.

Abb. 1–6. *Lutetiella hartkopfi* n. sp. Temporärer Aufschluss an der Straße B10 zwischen Birkweiler und Albersweiler, Rheinland-Pfalz. Eozän, Lutetium, Landauer Mergel. Der Maßstab stellt 2 mm für alle Ansichten gesamter Gehäuse dar, und 1 mm für die Ansichten der frühen Umgänge.

Abb. 1. Holotype (SMF 341586). Gehäuse mit großem und leicht 'eingezogenem' letzten Umgang; Umgänge mäßig konvex.
Abb. 2. Paratype (SMF 341588). Kleineres schlankes Gehäuse mit relativ kleiner Mündung; Parietalwand nur lose an das Gehäuse angeheftet, einen relativ großen Pseudumbilikus bildend; Umgänge stärker gewölbt.
Abb. 3. Paratype (SMF 341589). Gehäuse mit großer Schlusswindung und deutlich gewölbten Umgängen.
Abb. 4. Paratype (SMF 341590). Schlankes Gehäuse mit relativ kleiner Schlusswindung, kaum 'eingezogen', Umgänge mäßig gewölbt.
Abb. 5. Paratype (SMF 341591). Breites Gehäuse mit großer, kaum 'eingezogener' Schlusswindung, Umgänge mäßig gewölbt.
Abb. 6. Paratype (SMF 341587). Schlankes Gehäuse mit relativ kleiner, kaum 'eingezogener' Schlusswindung; Umgänge deutlich gewölbt.

kopfi has a lesser height, lesser aperture height and lesser breadth than *L. conica* (see Fig. 9a and Table 1 for values). The whorls are only occasionally subangulate, the suture is not appressed as in some individuals of *L. conica*, and the narrow umbilicus is usually open.

Table 1. Characters of *Lutetiella* species and comparison with *Peringia* and *Wallaua*.
Tabelle 1. Merkmale der *Lutetiella*-Arten und Vergleich mit *Peringia* und *Wallaua*.

	Lutetiella hartkopfi	***Lutetiella conica***	***Peringia ulvae***	***Wallaua flexiplicata***
Number of measured specimens	117	75	n/a	5
Protoconch 1				
preservation	corroded	strongly corroded	live larvae with periostracal shell only; mineralisation post-larval	well preserved
No. of whorls	0.40–0.55	0.75?	0,5	1
diameter [µm]	140–170	200?	140–150	340
diameter of nucleus [µm]	55–90	60–80?	40	100
shape	nearly planispiral	nearly planispiral	nearly planispiral	nearly planispiral
microsculpture	densely spaced, connected short wrinkles; and short spiral folds on later part	not preserved	very finely granulose	very finely granulose (1,6 µm)
boundary to protoconch 2 or teleoconch	change of sculpture; sometimes a constriction	gradual?	sharp change of sculpture; numerous "pitted plates" 2 µm wide	abrupt change of sculpture
Protoconch 2				
terminates after whorl	1.25–1.75	1.50–1.75?	1,5	absent
diameter [µm]			260–300	n/a
microsculpture	growth lines and broad, rounded spiral ribs; both may be obsolete	growth lines only?	periostracal shell with 14–17 spiral threads, very fine granulation and growth lines; after mineralisation spiral furrows and growth lines	n/a
boundary to teleoconch	gradual	gradual	sharp change of sculpture; a collabral rib on periostracal shell	n/a
Teleoconch				
No. of whorls (whole shell, max.)	6,5	7,15	7,8	5,2
height at 6,25 and 5,2 whorls	5.28/3.39	6.37/4.46	not determined due to heavy corrosion of apex	– /3.08
breadth at 6,25 and 5,2 whorls	3.04/2.15	3.54/2.62		– /1.88
height of last whorl at 6,25 and 5,2 whorls	3.77/2.54	4.48/3.28		– /2.28
aperture height at 6,25 and 5,2 whorls	2.28/1.59	2.73/2.06		– /1.30
sculpture on middle whorls	1st and 2nd order collabral growth striae, and more or less regular spiral striae, equal to 2nd order collabral striae	distant 1st order collabral striae, intercalated 3–5 2nd order striae, spirals in strength between 1st and 2nd order striae	distant 1st order collabral striae, intercalated 3–5 2nd order striae, all irregularly spaced; distant 1st order spirals and densely spaced very fine 2nd order spirals	subregular riblets
sculpture on last whorl	distant irregular 1st order collabral striae, 4–7 strong 2nd order striae, spiral striae subdued	as on middle whorls	as on middle whorls	subregular riblets, often every 4th to 5th riblet stronger
direction of growth lines	middle whorls slightly prosocline, towards aperture becoming opisthocyrt, with abapical part of peristome protracted	middle whorls slightly prosocline, towards aperture becoming opisthocyrt, with abapical part of peristome protracted	prosocline to orthocline	riblets orthocline to opisthocyrt
suture	moderately deep to shallow	moderately deep to nearly flush	nearly flush	deep
outline of whorls	either convex, stepped; or moderately convex, not stepped; middle whorls rounded	moderately to weakly convex, not stepped; middle whorls subangulate	weakly convex, not stepped, subangulate or rounded	convex, stepped
last whorl	rounded to weakly subangular	rounded to weakly subangular	subangular or rounded	rounded
aperture	either rounded pear- shaped (when whorl outline is stepped) or pear- shaped	pear-shaped	pear-shaped	oval

Table 1. Continued.
Tabelle 1. Fortsetzung.

	Lutetiella hartkopfi	***Lutetiella conica***	***Peringia ulvae***	***Wallaua flexiplicata***
umbilicus	narrow & open, or almost completely closed by shell material; columellar edge raised above umbilical area	none; columellar edge raised above umbilical area	closed; in adults columellar edge may form a pseudumbilicus	narrow, open
columellar edge	long, straight	long, slightly curved	long, curved	long, slightly curved
parietal callus	simple or thickened	thickened	simple or thickened	simple
palatal edge	shell wall tapering towards peristome; inner shell layers often ending before reaching peristome	shell wall tapering towards peristome; inner shell layers often ending before reaching peristome	simple	simple

Description: see Table 1.

Relationships: *L. conica* (Prévost 1821) has subangulate middle whorls, the umbilicus is always closed, the shells are slightly more slender and can grow larger. On the basis of measurements alone it could be argued that *L. hartkopfi* is merely a population of *L. conica* which does not reach the full size of the latter, but when the number of whorls is considered, it is evident that at any given number of whorls the dimensions of *L. hartkopfi* are smaller than those of *L. conica*.

Comments: (1) A relatively large variability is admitted in this species as it proved impossible to separate the individuals consistently into several species. The morphological contrast between slender conical forms with an open umbilicus, convex whorls and a relatively small aperture, and conico-ovate ventricose forms with closed umbilicus, barely convex whorls and a large aperture is striking, but intermediate character combinations are also common (Figs. 1–6). As similar tendencies were also observed in *Lutetiella conica*, it is concluded that such variability is inherent in this genus. A possible explanation is sexual dimorphism, which is reported in Cochliopidae (e.g. *Tryonia porrecta* (Mighels 1845) (Hershler et al. 2007)), and Hydrobiidae (*Mercuria* spp. (Giusti in litt.); *Hydrobia acuta neglecta* Muus 1963 and *Ecrobia ventrosa* (Montagu 1803) (Bishop 1976)).

(2) The sculpture of protoconch 2 is strongly variable: growth lines and spiral ribs are well developed to nearly absent. This, and the variable shapes of the juvenile shells suggests a variable and probably often stressful environment.

Lutetiella conica (Prévost 1821)

Figs. 9–15, Tab. 1

Literature references; the earliest report of a locality is cited, plus the locality of figured specimens):

non 1810 Bulime conique – Brard: 416, pl. 24 fig. 14–17 ("On trouve ce joli fossile dans les silex coquilliers des environs de Lagny, et à St.-Leu Taverny, dans la même pierre qui renferme des lymnées et des cérites.") [unavailable name: vernacular]

non 1814 *Paludina conica* Férussac: 64, no. 11 ("Lagny. Les environs de Paris. Formation inconnue")

* 1821 *Paludina conica* Prévost: 427 (spoils of a shaft dug to drain "… une carrière de calcaire à cérites, exploité à l'extrémité de la plaine de Mont-Rouge, très-près du château de Bagneux, un peu avant le chemin de traverse qui conduit de ce dernier village à la route d'Orléans.")

• 1824 *Paludina conica* – Deshayes: 128, pl. 16 fig. 6–7 (Vaugirard, Septeuil (marne blanche, coll Héricart-Ferrand); "C.Prévost … a fait connaître deux nouvelles espèces de Paludines dont la découverte est due à M. Desnoyers." and "Nous devons ceux [individus] de Vaugirard à l'obligeance de MM. Prévost et Desnoyers.")

• 1832 *Paludina conica* – Deshayes: 693–694

1838 *Paludina conica* – Deshayes in Lamarck: 324

? 1839 *Bulimus conicus* – Mantell: 232, pl. 39 fig.1–2 (Paris Basin)

1850 *Paludestrina conica* – d'Orbigny: 412

1862 *Bithinia conica* – Deshayes: 494–495, no. 7 (Calcaire grossier supérieur: Maule, Beyne, la Ferme de l'Orme, Grignon, Passy, Cumières, Boursault, Gomerfontaine; Sables moyens: Verneuil, Chéry-Chartreuve, la Chapelle en Serval; Calcaire de Saint-Ouen: Saint-Aubin près Mans)

1870 *Assiminea conica* – Sandberger: pl. 11 fig. 11–11b (F. 11: Gomerfontaine)

1871 *Assiminea conica* – Sandberger: pl. 15 fig. 12–12b [Sandberger 1872 (: 212) quotes this erroneously as fig. 9–9b] (F. 12: Saint-Aubin near Le Mans, Calcaire de St. Ouen)

1872 *Assiminea conica* – Sandberger: 212–213, 254

1888 *Assiminea* (*Assiminea*) *conica* – Cossmann: 205 (Separate: 209) (Neauphlette, Auvers, Valmondois)

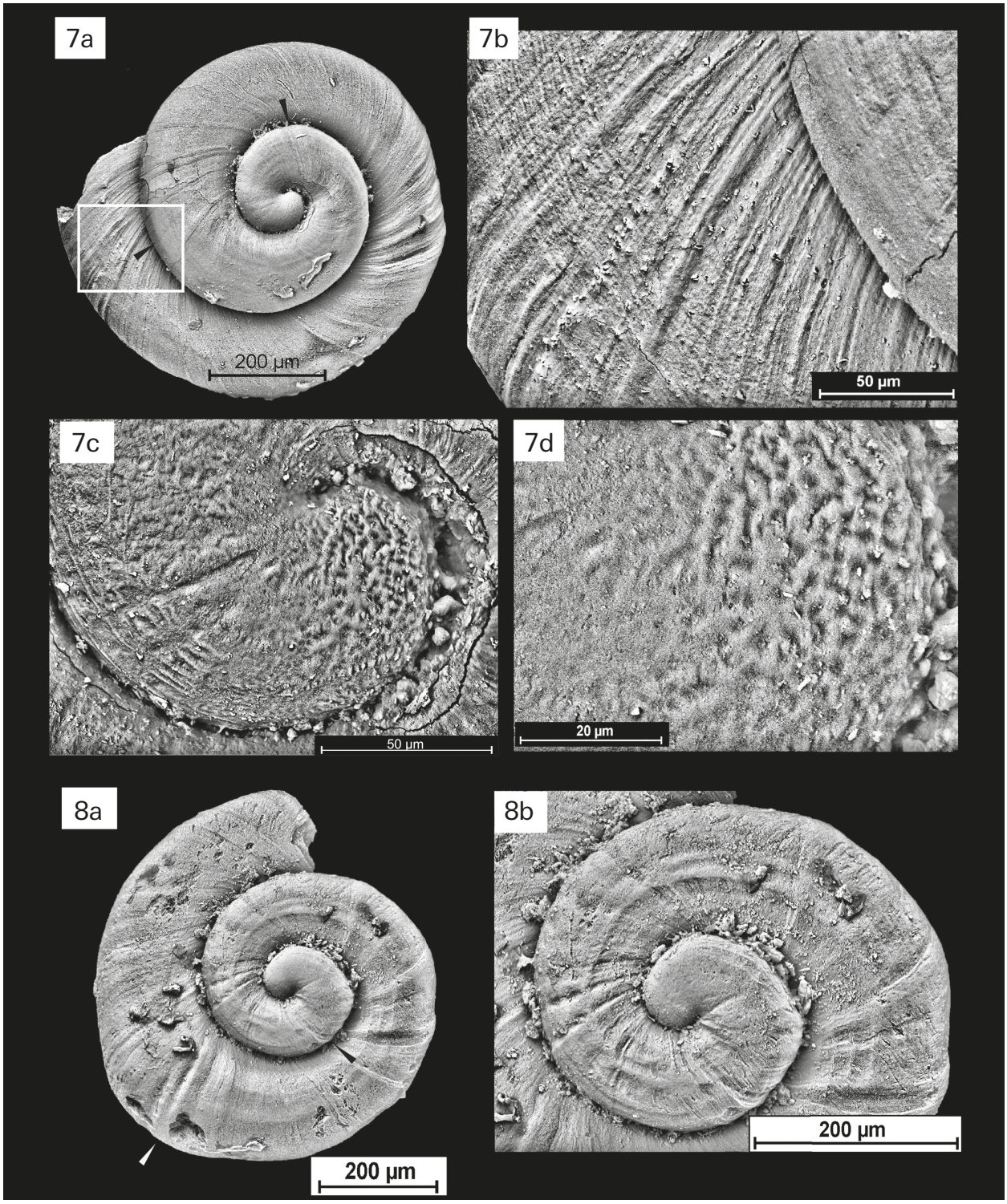
1900 *Assiminea conica* – Cossmann & Pissarro: 212, pl. 22, fig. 23

1910 *Assiminea conica* – Cossmann & Pissarro: pl. 13 fig. 83.1 (Neauphlette, "Lut. (Bart.)")

1913 *Peringia conica* – Cossmann: 124

1921 *Peringia* (*Peringia*) *conica* – Cossmann: 132, pl. 3, fig. 99–100 (Pacy-sur-Eure)

• 1926 *Peringia conica* – Wenz: 1978–1980 (Calcaire grossier supérieur: Cresnes, Parnes, Paissy, Pont-Bernard, Douains, Fresville, Hauteville; Sables moyens de Beau-



champ: Munneville, Sognolles-Frépillon) [here additional 37 references for the period 1825–1913, plus 7 for localities outside the Paris Basin, which are all misidentifications]

• 1947 *Assiminea conica* – Furon & Soyer: 109, 156

1962a *Peringia conica* – Glibert: 32 (IRSNB Material: Lutétien: Bréval, Ferme de l'Orme, Ferme du Pré, Gomerfontaine, Neauphlette, Hermonville, Parnes, Plessis-Hébert, Fresville- Auversien: Le Fayel)

1980 *Peringia conica* – C. Dolin et al.: 27 (Baron (Déptm. Oise): Bartonien)

1995 *Peringia conica* – Le Renard & Pacaud: 98, no. GA 83-1 (checklist)

1996 *Hydrobia* (*Peringia*) *conica* – Pacaud & Le Renard: 160 (checklist)

• 2008 *Peringia conica* – Pacaud: 54 (Lutetian checklist)

Figs. 7–8. *Lutetiella hartkopfi* n. sp. Temporary exposure at the road B10 between Birkweiler and Albersweiler, Rhineland-Palatinate, Germany. Eocene, Lutetian, Landauer Mergel. Protoconch and early teleoconch microsculptures of juvenile specimens. Arrows in Figs. 7a and 8a indicate boundaries of protoconch 1 and protoconch 2.

Fig. 7. Specimen with best preserved protoconch 1 microsculpture. Protoconch 1 with spiral crests (Fig. 7c) and broad, but very flat spiral ribs (Fig. 7a). Protoconch 2 with faint and regular growth lines and very weak spiral ribs. Boundary to teleoconch indistinct (SMF 344883).

Fig. 8. Specimen with strong sculpture development on protoconch 2. Boundaries of protoconch 1 and 2 distinct. Note growth lines of variable amplitude and strong spiral ribs on protoconch 2 (SMF 344884).

Abb. 7–8. *Lutetiella hartkopfi* n. sp. Temporärer Aufschluss an der Straße B10 zwischen Birkweiler und Albersweiler, Rheinland-Pfalz. Eozän, Lutetium, Landauer Mergel. Protokonch- und frühe Teleokonch-Mikroskulpturen juveniler Exemplare. Pfeile in Abb. 7a und 8a bezeichnen die Grenzen von Protokonch 1 und Protokonch 2.

Abb. 7. Exemplar mit der am besten erhaltenen Protokonch 1-Mikroskulptur. Protokonch 1 mit spiraligen Kielen (Abb. 7c) und breiten sehr flachen Spiralrippen (Abb. 7a). Protokonch 2 mit sehr schwachen und regelmäßigen Anwachslinien und sehr schwachen Spiralrippen. Grenze zum Teleokonch undeutlich (SMF 344883).

Abb. 8. Exemplar mit kräftiger Skulpturentwicklung auf Protokonch 2. Grenzen von Protokonch 1 und 2 deutlich. Protokonch 2 mit Anwachslinien variabler Amplitude und mit starken Spiralrippen (SMF 344884).

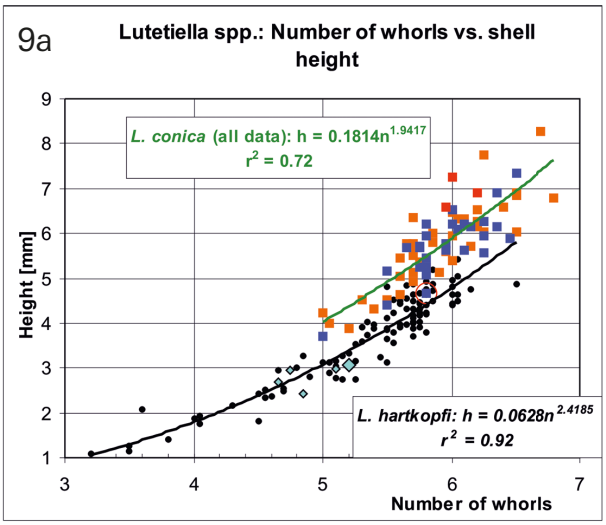
Nomenclature: The name „*Paludina*“ *conica* Prévost 1821 has since its inception been used frequently and consistently for the species here described. There exists, however, the senior homonym „*Paludina*“ *conica* Férussac 1814[1], which had been completely overlooked in the literature and has therefore not been used as the valid name of any taxon. For its possible identity see further discussion below. The conditions stipulated in Article 23.9 ICZN for the reversal of precedence to protect the usage of a junior homonym are not met, however, as the name *conica* Prévost has not been used 25 times in the past 50 years. To facilitate the continuing use of the binomen *Lutetiella conica*, an application has been made to the International Commission for Zoological Nomenclature to suppress the name *Paludina conica* Férussac 1814 (Kadolsky, in press).

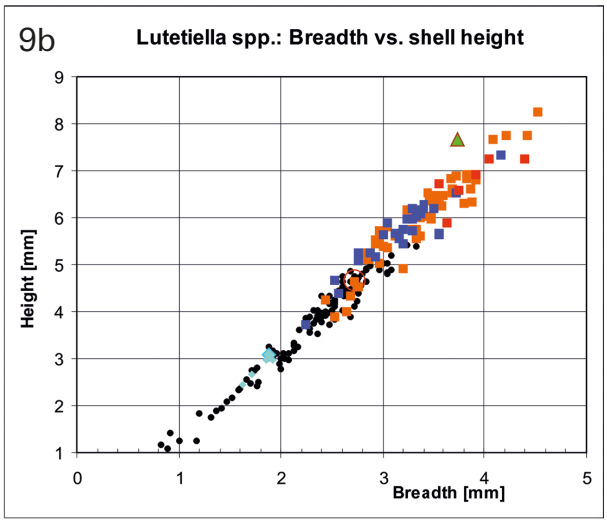
J. M. Pacaud (MNHN Paris, in litt. 14. Jan. 2013) favoured the interpretation of *Paludina conica* Férussac as both a senior homonym and synonym of *Paludina conica* Prévost. However, analysis of the original publications of Brard (1810) and Férussac (1814) does not support this interpretation: Férussac (1814: 64) introduced the nominal species *Paludina conica* by a reference to the description and figure of “Bulime conique” by Brard (1810). Brard’s species is, according to the figures, an elongate conical hydrobioid of approximately 7.7 mm shell height. Its whorls are numerous, with convex outlines, and the aperture is relatively small. Measurements taken from the original figures show for every parameter significant deviations from the values of the *Lutetiella hartkopfi*/*conica* complex (Fig. 9b–e). This is most obvious when ratios are plotted, indicating that the entire shell habitus is significantly different (Fig. 9d–e). The localities given by Brard (1810) appear to be erroneous. At the locality Lagny, only fossils attributable to the Sparnacien (“Lignites”) have subsequently been reported (Wenz 1928: 2379, 2392). At Brard’s Saint-Leu Taverny, which is now called Saint-Leu-la-Forêt-et-Taverny (Département Val d’Oise), outcrops of the Early Rupelian Meulières de Montmorency are extensive. This formation consists of claystones with large silicified concretions (meulières = millstones), which contain commonly lymnaeids, planorbids, small hydrobioids and *Potamides lamarkii* Brongniart 1810. This is consistent with Brard describing the ‘Bulime conique’ occurring with planorbids and “cerithids” (possibly *Potamides lamarkii*) in silicified rocks. Although this could be seen as an indication that Brard actually described a hydrobioid from the Meulières de Montmorency, no hydrobioid of the large size given by Brard (height 7.7 mm) has ever been discovered in this formation. Wenz (1923–30) compiled the published occurrences of fossil non-marine mollusks from this locality under the erroneous names “Saint Leu d’Esserent” and “Saint Leu d’Esserent-Taverny”[2], and attributed them to the Meulières de Montmorency only.

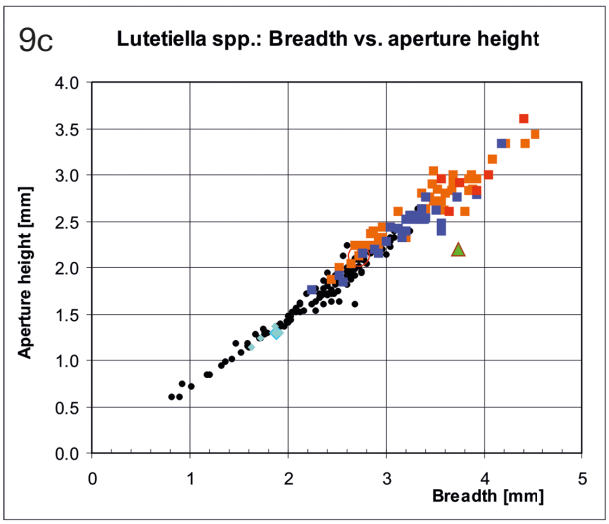
In the literature post 1814, the name „*Paludina*“ *conica* Férussac has apparently not been used, whether as

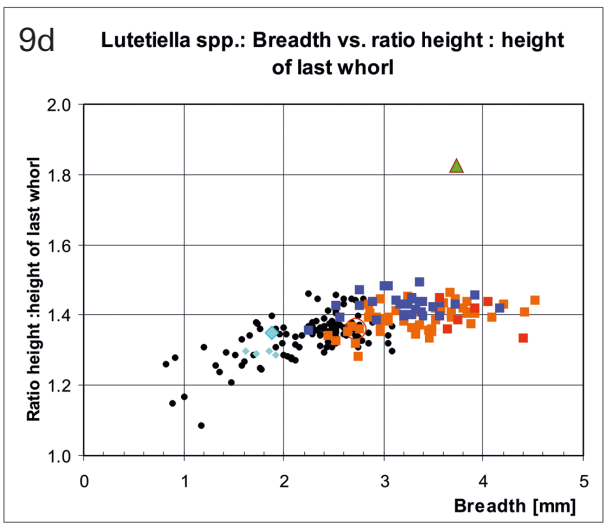
[1] Férussac quotes his species as “*C. Conica*. Brard (Bul.)”. The “C.” stands for *Cyclostoma*, but this is treated as an error, as the species is listed under the heading of *Paludina*. Thus Férussac’s intention was to assign Brard’s species to the genus *Paludina*.

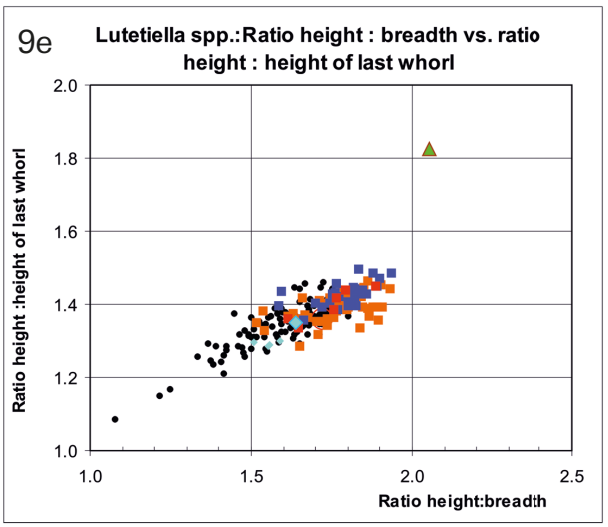
[2] Wenz confused two localities with similar names: Saint-Leu-d’Esserent in the Département Oise, ca. 45 km NNE Paris, and Saint-Leu-la-Forêt-et-Taverny in the Département Val d’Oise, at the NW periphery of Paris. At the former locality outcrops of Lutetian strata have been described (Blondeau & Cavelier 1962, 1963), but there is no published record of *Lutetiella conica*; the latter locality is situated at the edge of the Forêt de Montmorency in the type area of the Rupelian Meulières de Montmorency.

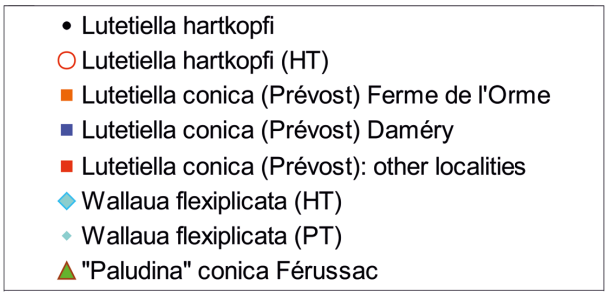












the name of a taxon considered valid, or as a synonym, with the possible exception of Mantell (1839), who used Brard's genus attribution in its latinized form. The species has not been found again at either of the two original localities, with their vastly different outcrop stratigraphy. Any attempt at identification would probably involve to select arbitrarily a neotype with a new type locality and type stratum. Because of the antiquity of Férussac's name, it would then most likely replace a junior, and better defined name.

Fig. 9. Shell measurements and measurement ratios of *Lutetiella hartkopfi* n. sp. and *L. conica* (Prévost). For reference, data from *Wallaua flexiplicata* R. Janssen and from Brard's figures of „*Paludina*" *conica* Férussac are included.

Fig. 9a. Shell height vs. number of whorls. This gives the clearest separation of *L. hartkopfi* and *L. conica*. Plots of breadth, aperture height and height of last whorl against number of whorls show a similar separation, showing that the shells of the two species grew according to different parameters.

Fig. 9b. Shell breadth vs. shell height is a nearly linear relationship. *L. conica* has the same proportions as *L. hartkopfi*, but grows to a larger size. „*Paludina*" *conica* Férussac is outside this trend.

Fig. 9c. Shell breadth vs. aperture height. Same relationship as in Fig. 9b.

Fig. 9d. Shell breadth vs. ratio shell height : height of last whorl. Below 2.4 mm shell breadth, the changing ratios indicate that shell growth is allometric. At larger shell sizes the proportions remain nearly constant. Note difference between the populations of *L. conica* from Daméry and Ferme de l'Orme. „*Paludina*" *conica* Férussac is widely outside the *Lutetiella* trend.

Fig. 9e. Ratio shell height : shell breadth vs. ratio shell height : height of last whorl. This plot ignores growth allometries. It shows that with increasingly slender shells the relative height of the last whorl decreases. *L. conica* tends to have more slender shells than *L. hartkopfi*, but there is a wide overlap. Again, „*Paludina*" *conica* Férussac is widely outside the *Lutetiella* trend.

Abb. 9. Gehäusemaße und Verhältniszahlen von *Lutetiella hartkopfi* n. sp. und *L. conica* (Prévost). Zum Vergleich sind Daten von *Wallaua flexiplicata* R. Janssen und von Brards Abbildung der „*Paludina*" *conica* Férussac eingefügt.

Abb. 9a. Gehäusehöhe zu Windungszahl. Diese Parameter unterscheiden *L. hartkopfi* und *L. conica* am deutlichsten. Diagramme von Breite, Mündungshöhe und Höhe der Schlusswindung gegen Umgangszahl zeigen ähnliche Trennungen. Dies zeigt, dass das Gehäusewachstum der zwei Arten nach unterschiedlichen Parametern erfolgte.

Abb. 9b. Gehäusebreite zu Gehäusehöhe: eine nahezu lineare Funktion. *L. conica* hat die gleichen Gehäuseproportionen wie *L. hartkopfi*, erreicht aber eine größere Größe. „*Paludina*" *conica* Férussac liegt außerhalb dieses Trends.

Abb. 9c. Gehäusebreite zu Mündungshöhe: Beziehungen wie in Abb. 9b.

Abb. 9d. Gehäusebreite zu Verhältnis Gehäusehöhe : Höhe der Schlusswindung. Bei unter 2,4 mm Gehäusebreite zeigen die veränderlichen Verhältniszahlen, dass das Gehäusewachstum allometrisch ist. Bei größerrer Gehäusebreite bleiben die Proportionen fast konstant. Beachtenswert ist ein Unterschied zwischen den Populationen der *L. conica* von Daméry und von Ferme de l'Orme. „*Paludina*" *conica* Férussac liegt weit außerhalb des *Lutetiella*- Trends.

Abb. 9e. Verhältnis Gehäusehöhe : Gehäusebreite zu Verhältnis Gehäusehöhe : Höhe der Schlusswindung. In diesem Diagramm wird Wachstumsallometrie ignoriert. Es zeigt, dass bei zunehmender Schlankheit des Gehäuses die relative Höhe der Schlusswindung abnimmt. *L. conica* tendiert zu schlankeren Gehäusen als *L. hartkopfi*, jedoch existiert eine große Überlappungszone. Auch hier liegt „*Paludina*" *conica* Férussac weit außerhalb des *Lutetiella*- Trends.

Type material and locality: Prévost describes his material coming from the spoil heap of a drainage shaft dug in a quarry in the Calcaire grossier near the chateau of Bagneux and in the vicinity of the village of Mont-Rouge (now spelled Montrouge). Although he did not observe in situ the stratigraphic succession in which *L. conica* occurred, he inferred that it occurred below the Calcaire grossier, although the subsequent authors always reported to this species as occurring within the Calcaire grossier. Curiously, Deshayes (1824) stated that Desnoyers discovered this species at Vaugirard, although Prévost conveyed the impression that he discovered it himself, and not at Vaugirard. Deshayes (1824) stated that he received specimens from Vaugirard by Prévost as well as Desnoyers, but as far as Prévost's material is concerned, this appears to be an error by Deshayes, unless Prévost acquired specimens from Vaugirard after his publication. Both Vaugirard and Montrouge are now completely built-up parts of Paris, approximately 3 km apart. Curiously, Wenz (1926) omitted both localities, Bagneux/Montrouge and Vaugirard, in his generally comprehensive compilation of localities.

Specimens from Vaugirard were examined (Fig. 12) and found to agree with the species concept as established in the literature.

Material studied:

Calcaire grossier, Lutetian:

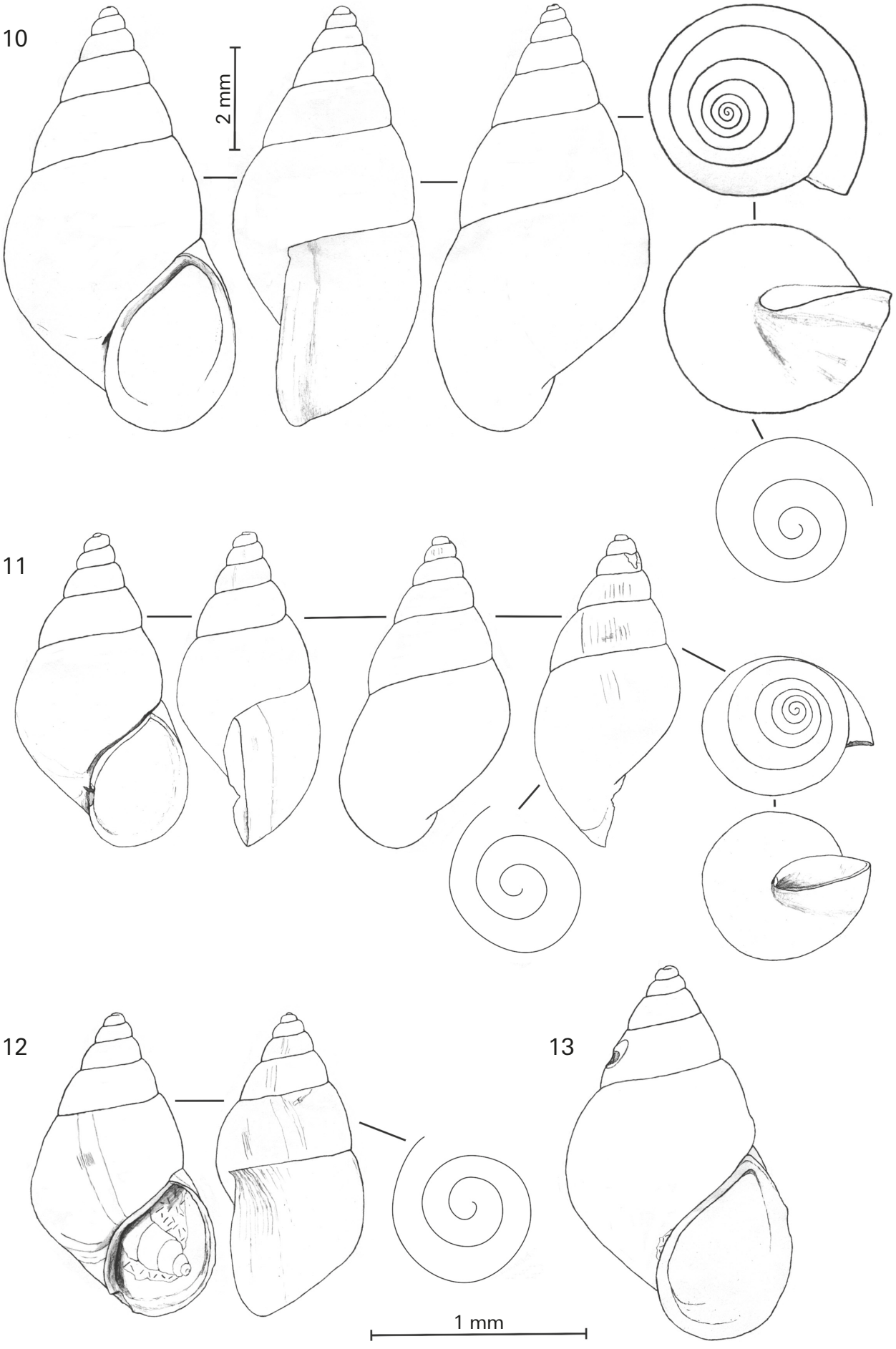
- Vaugirard, 12 specimens: NHMUK 32080.
- Passy?, 9 specimens: MNHN Paris B59.275, coll. Tournouer.
- Villiers-St-Frédéric, 1 specimen: Coll. Le Renard no. 54491.
- La Ferme de l'Orme, 2 specimens: Coll. Le Renard no. 54372. 52 specimens: SMF 267779.
- Daméry, 8 specimens: coll. Le Renard no. 56236. 29 specimens: SMF 267780.
- Neauphlette, 2 specimens: NHMUK G5787.

Sables de Beauchamps, Bartonian:

- Beauchamps, 1 specimen: NHMUK G89469.

Description: see Table 1.

Variability: The plots of shell parameters (Fig. 9a–e) show a greater variability than in *Lutetiella hartkopfi* n. sp., as individuals from several localities are presented. The ratio height : breadth and the relative aperture height vary in a similar way as in *Lutetiella hartkopfi* n. sp. Immature specimens have often subangulate whorls, which usually, but not always become rounded in adults. The thickness of the parietal callus is variable. The spiral


10
2 mm
11
12
13
1 mm

Figs. 10 – 13. *Lutetiella conica* (Prévost 1821). Eocene, Lutetian, Calcaire grossier in the Paris Basin. The 2 mm scale applies to all views of whole shell. 1 mm scale applies to apical views of early whorls.

Fig. 10. La Ferme de l'Orme. Coll. Le Renard (LR 54372).
Fig. 11. Daméry. Coll. Le Renard (LR 56236).
Fig. 12. Vaugirard (MNHUK 32080).
Fig. 13. Passy. Coll. Tournouer (MNHN Paris B 59.275).

Abb. 10 – 13. *Lutetiella conica* (Prévost 1821). Eozän, Lutetium, Calcaire grossier des Pariser Beckens. Der 2 mm-Maßstab gilt für alle Ansichten ganzer Gehäuse. Der 1-mm-Maßstab gilt für die Apikalansichten der frühen Windungen.

Abb. 10. La Ferme de l'Orme. Sammlung Le Renard (LR 54372).
Abb. 11. Daméry. Sammlung Le Renard (LR 56236).
Abb. 12. Vaugirard (MNHUK 32080).
Abb. 13. Passy. Sammlung Tournouer (MNHN Paris B 59.275).

sculpture varies in strength (Figs.14 – 15). The last whorl is in most individuals not 'pulled in' relative to the preceding whorl, but in some individuals from Daméry this feature is well developed, resulting in a more oval shell shape (Fig. 11, 14)

Distribution: Lutetian (Calcaire grossier) and Bartonian (Sables de Beauchamps, Calcaire de Saint Ouen), Paris Basin.

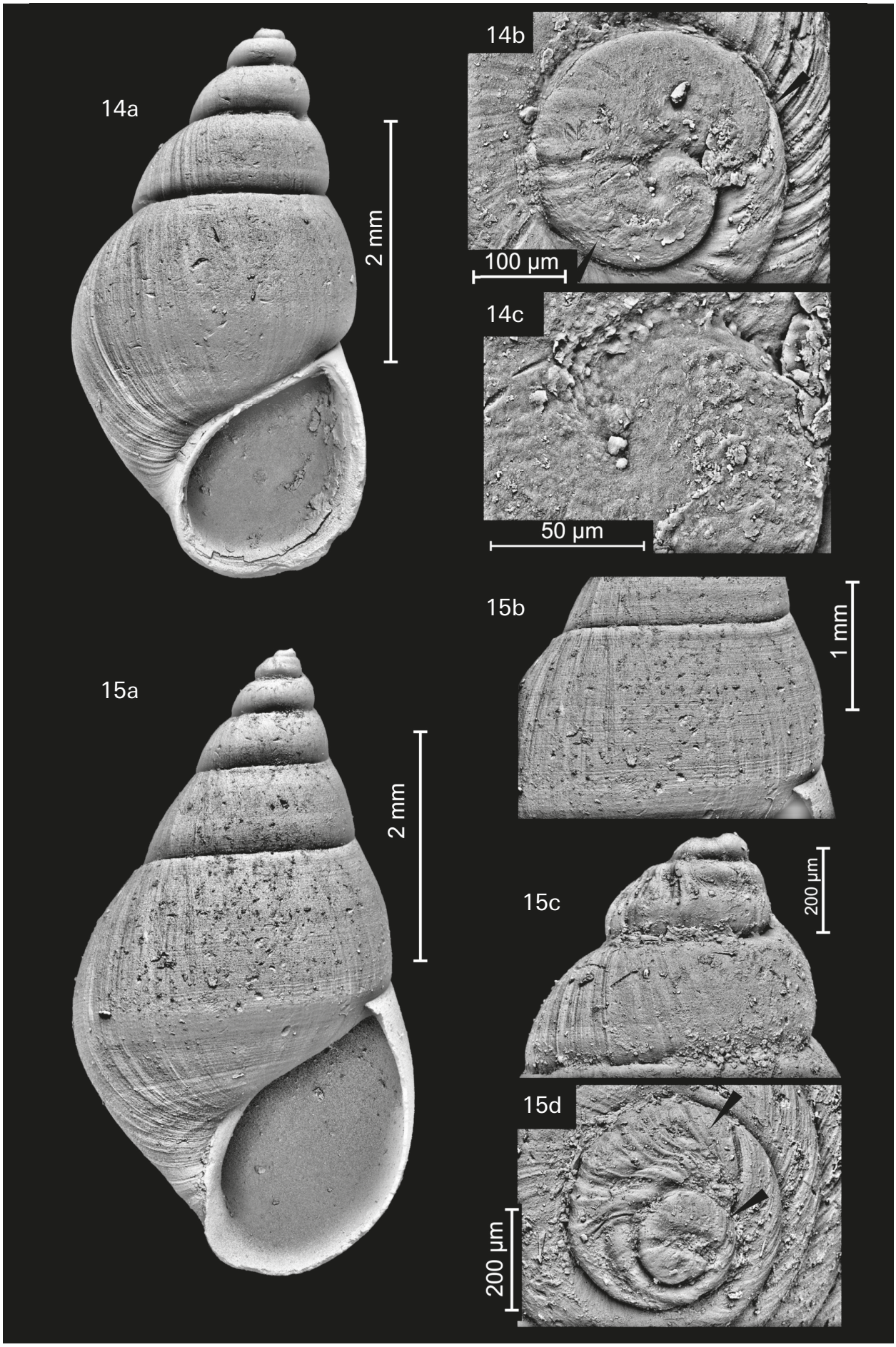
Conclusions

Palaeoenvironment: *Lutetiella* species are known from molluscan associations of very low diversity. *L. hartkopfi* forms almost monospecific assemblages (more than 99% of the assemblages); very rare accessory species include Potamididae sp.indet., "*Hydrobia*" sp. and Viviparidae sp. indet. Taphonomic observations indicate that the fauna is allochthonous (Kadolsky & Hartkopf-Fröder, in prep.), i.e. it is unknown whether any or all of these species lived in the same habitat. Completely absent are the freshwater groups which always dominate pure freshwater associations: Lymnaeidae and Planorbidae. This and the very low diversity suggests a brackish environment of very low salinity.

Lutetiella conica occurs in a few horizons of the Paris Basin Lutetian, where it is associated with *Stalioa desmarestii* (Prévost 1821), another hydrobioid of uncertain affinities. Prévost (1821) describes it from a black, earthy lignite, in which they are associated with Planorbidae, Lymnaeidae, *Potamides*, other hydrobioids („*Bulimus*") and Mytilidae species. A similar low salinity brackish habitat is here, too, likely.

Biogeography: The difference at the species level between *Lutetiella hartkopfi* n. gen. n. sp. of the Rhine Graben and *L. conica* of the Paris Basin may be due to an age difference within the same lineage, considering the long duration of the Lutetian of 6.6 m.a., or due to endemism. This case is analogous to the relationship in the freshwater hydrobioid genus *Euchilus* Sandberger 1871, which in the Lutetian of the Paris Basin (Calcaire de Provins, St. Parres) is represented by *E. deschiensianus* (Deshayes 1862), and in the Lutetian of the Rhine Graben area (freshwater limestone of Bouxwiller) by *E. gregarius* (Wenz 1926), as redefined by Kadolsky (1993).

As the Paris Basin and the Rhine Graben were unconnected during the Lutetian (Gély 2008), endemism is a probable cause of the species differences. The possibility of a brackish inland lake in the Rhine Graben during the Eocene, without direct connection to any open sea may also be considered, analogous to the Late Oligocene and Early Miocene formations of the northern Rhine Graben (Kadolsky 1989).


14a
2 mm
14b
100 µm
14c
50 µm
15a
2 mm
15b
1 mm
15c
200 µm
15d
200 µm

Figs. 14–15. *Lutetiella conica* (Prévost 1821). Eocene, Lutetian, Calcaire grossier in the Paris Basin. Arrows point to the boundaries of protoconch 1 and protoconch 2. Protoconch surfaces lacking details of the microsculpture due to corrosion.

Fig. 14. Daméry (SMF 267790). Relatively slender shell with 'pulled-in' last whorl and convex whorls. Protoconch 2/teleoconch boundary clearly demarcated; on protoconch 1 possible relics of wrinkly microsculpture similar to that of *L. hartkopfi* (compare Figs. 7c–d).

Fig. 15. Ferme de l'Orme (SMF 267779). Relatively broad shell with large last whorl which is subangulate; shell with regular conical shape and hardly convex whorls. Spiral sculpture strong, parietal wall not developed. Traumatic deformation of protoconch 2, with strong growth lines.

Abb. 14–15. *Lutetiella conica* (Prévost 1821). Eozän, Lutetium, Calcaire grossier des Pariser Beckens. Pfeile zeigen auf die Grenzen von Protokonch 1 und Protokonch 2. Den Protokonch- Oberflächen fehlen Details infolge Korrosion.

Abb. 14. Daméry (SMF 267790). Relativ schlankes Gehäuse mit 'eingezogener' Schlusswindung und gewölbten Umgängen. Grenze Protokonch 2/ Teleokonch deutlich markiert; auf Protokonch 1 möglicherweise Relikte runzeliger Mikroskulptur ähnlich der von *L. hartkopfi* (vgl. Abb. 7c–d).

Abb. 15. Ferme de l'Orme (SMF 267779). Relativ breites Gehäuse mit großer subangulater Schlusswindung; Gehäuse von regelmäßig konischer Gestalt mit kaum gewölbten Umgängen. Spiralskulptur stark, Parietalwand nicht ausgebildet. Traumatische Deformation des Protokonchs 2, mit starken Anwachslinien.

Acknowledgements

Christoph Hartkopf-Fröder (Geologischer Dienst Nordrhein-Westfalen, Krefeld) initiated this study and provided the Birkweiler material. He and Folco Giusti (Dipartimento di Scienze Ambientali, Università degli Studi di Siena) provided most, respectively some of the SEM micrographs of *Lutetiella hartkopfi* and *L. conica*. Dr. Peter Schäfer (Landesamt Rheinland-Pfalz für Geologie und Bergbau) provided the mollusks from a control boring near the Birkweiler outcrop. Jean-Michel Pacaud (Muséum National d'Histoire Naturelle, Département Histoire de la Terre, Paris) shared his views on the nomenclature of *Paludina conica* and provided information about localities in the Paris Basin. Dr. Ronald Janssen (Forschungsinstitut Senckenberg, Frankfurt a. M.), Jacques Le Renard, Prof. Agnès Rage and Jean-Michel Pacaud (Muséum National d'Histoire Naturelle, Paris) and Dr. Paul Jeffery (Natural History Museum, London) facilitated loans of reference material. Their support is gratefully acknowledged.

References

Notes: (1) Information on the precise dates of publication are added in angular brackets with the following conventions: dates without additional information are those printed in the cited work; library date stamps are from copies in the libraries of the Natural History Museum London (NHMUK) and of the Geological Society of London (GSL). (2) Plates and enclosures are cited when they are not included in the numbered pages of the cited work.

Anderson, H.-J. (1960): Die Gastropoden des jüngeren Tertiärs in Nordwestdeutschland. Teil 2: Prosobranchia Mesogastropoda. 1: Littorinacea, Rissoacea, Cerithiacea. – Meyniana, **9**: 13–79. [III. 1960].

Anderson, H.-J. (1964): Die miocäne Reinbek-Stufe in Nord- und Westdeutschland und ihre Mollusken-Fauna. – Fortschr. Geol. Rheinl. Westf., **14**: 31–368. [XII.1964].

Bandel, K. (1975): Embryonale und larvale Schale einiges Prosobranchier (Gastropoda, Mollusca) der Oosterschelde (Nordsee). – Hydrobiol. Bull., **9** (1): 3–22. [IV.1975].

Bank, R.A.; Butot, L.J.M. (1984): Some more data on *Hydrobia ventrosa* (Montagu, 1803) and „*Hydrobia*" *stagnorum* (Gmelin, 1791) with remarks on the genus *Semisalsa* Radoman, 1974. – Malakol. Abh. staatl.Mus. Tierkde. Dresden, **10** (2): 5–15. [1.10.1984].

Bishop, M.J. (1976): *Hydrobia neglecta* in the British Isles. – J. Mollusc. Stud., **42**: 319–326.

Blondeau, A.; Cavelier, C. (1962): Étude du Lutétien inférieur de Saint-Leu-d'Esserent (Oise). – Bull. Soc. géol. France, Sér. 7, **4** (2): 55–63. [XII. 1962].

Blondeau, A.; Cavelier, C. (1963): Étude du Lutétien inférieur a Boissy – Saint-Leu-d'Esserent (Oise). – Bull. Soc. géol. France, Sér. 7, **4** (2): 222–225. [III. 1963].

Bouchet, P.; Rocroi, J.-P. (2005): Classification and nomenclator of Gastropod families. – Malacologia, **47** (1–2): 1–397. [received 5.9.2005].

Brard, P. (1810): Second mémoire sur les lymnées fossiles des environs de Paris, et sur les coquilles qui les accompagnent. – Ann. Mus. Hist. natur., **15**: 406–421, pl. 24.

Cossmann, M. (1888a): Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. – Ann. Soc. roy. malacol. Belg., **23**: 3–324, pl. 1–12.

Cossmann, M. (1888b): Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris: 3–328, pl. 1–12 [Reprint of Cossmann 1888a; pagination: 1888a + 4].

Cossmann, M. (1899): Mollusques éocéniques de la Loire-Inférieure. Tome 2e, premier fascicule. – Bull. Soc. Sci. natur. Ouest France, **9** (4): 307–360, pl. 22–26. [date stamp NHMUK 22.3.1900].

Cossmann, M. (1913): Appendice No. 5 au Catalogue illustré des coquilles fossiles de l'Éocène des environs de Paris. – Ann. Soc. roy. zool. malacol. Belg., **49**: 19–238, pl. 1–8. [X. 1913]

Cossmann, M. (1921): Essais de paléoconchologie comparée, **12**: 345 [+2] pp., pl. A–D, pl. 1–6. Paris (M. Cossmann) [IV. 1921].

Cossmann, M.; Pissarro, G. (1900): Faune éocénique du Cotentin (Mollusques). – Bull. Soc. géol. Normandie, **19**: 19–75, pl. 1–6.

Cossmann, M.; Pissarro, G. (1907–1913): Iconographie complète des coquilles fossiles de l'Éocène des environs de Paris, **2**: 1907: pl. 1–9; 1910: pl. 10–25; 1911: pl. 26–45; 1913: pl. 46–65. Paris.

Criscione, F.; Ponder, W.F. (2013): A phylogenetic analysis of rissooidean and cingulopsoidean families (Gastropoda: Caenogastropoda). – Molec. Phylogenet. Evol., **66** (3): 1075–1082. [III. 2013].

Davis, G.M. (1979): The origin and evolution of the gastropod family Pomatiopsidae, with emphasis on the Mekong River Triculinae. – Monogr. Acad. natur. Sci. Philadelphia, **20**: VIII + 120 pp.

Davis, G.M.; Mazurkiewicz, M.; Mandracchia, M. (1982): *Spurwinkia*: morphology, systematics, and ecology of a new genus of North American marshland Hydrobiidae (Mollusca: Gastropoda). – Proc. Acad. natur. Sci. Philadelphia, **134**: 143–177.

Deshayes, G.P. (1824–1837): Description des coquilles fossiles des environs de Paris, **2** [Gastéropodes]: 1824: 1–178; 1833: 179–306; 1834: 307–434; 1835: 435–562; 1836: 563–690; 1837(a): 691–814; 1837(b): Atlas: 51 pp., 106 pl.; Paris (Deshayes; Béchet Jeune; Baudouin; Treuttel & Wurtz).

Deshayes, G.P. (1830–1832): Histoire naturelle des vers, des mollusques, des coquillages et des zoophytes: Encyclopédie méthodique, **2** (1): 1–256 (1830); **2** (2):257–594 (1831); **2** (3): 595–1152 (1832); Paris.

Deshayes, G.P. (1861–1863): Description des animaux sans vertèbres découverts dans le bassin de Paris, **2**: Livr. 21, 22: 1–120, pl. 1–5 (24.1.1861); Livr. 23, 24: 121–192, pl. 6–15 (22.5.1861); Livr. 25, 26: 193–312, pl. 16–20 (30.7.1861); Livr. 27, 28: 313–432, pl. 21–26 (20.11.1862); Livr. 29, 30: 433–544, pl. 27–31 (31.5.1862); Livr. 31, 32: 545–640, pl. 32–39 (15.11.1862); Livr. 33, 34: 641–736, pl. 40–46 (2.6.1863); Livr. 35, 36: 737–824, pl. 47–54 (5.8.1863); Livr. 37, 38: 825–920, pl. 55–62 (1.11.1863); Livr. 39, 40: 921–968, pl. 55–62 (1.11.1863); Paris (Baillière) [Publication dates at end of vol. 3].

Dolin, C.; Dolin, L.; Le Renard, J. (1980): Inventaire systématique des mollusques de l'Auversien à «faciès charrié» de Baron (Oise), et remarques paléontologiques. – Bull. inf. Géolog. bass. Paris, **17** (2): 26–48, 3 pl. [date stamp GSL 31.10.1981].

Fish, J.D.; Fish, S. (1977): The veliger larva of *Hydrobia ulvae* with observations on the veliger of *Littorina littorea* (Mollusca: Prosobranchia). – J. Zool., **182** (4): 495–503. [12.8.1977].

Fukuda, H.; Ponder, W.F. (2003): Australian freshwater assimineids, with a synopsis of the recent genus-group taxa of the Assimineidae (Mollusca: Caenogastropoda: Rissooidea). – J. natur. Hist., **37** (16): 1977–2032. [date stamp NHMUK: 26.11. 2003].

Fukuda, H.; Ponder, W.F. (2006): *Conassiminea*, a new genus of the Assimineidae (Caenogastropoda: Rissooidea) from southeastern Australia. – J. mollusc. Stud., **72** (1): 39–52. [II. 2006].

Férussac, A.E.J.P.J.F. d.d.f. (1814): Mémoires géologiques sur les terrains formées sous l'eau douce par les débris fossiles des mollusques vivants sur la terre ou dans l'eau non salée: 76 pp.; Paris (Poulet) [Author name fide Wenz 1923; on title page as J. Daudebart [sic] de Férussac. Includes: Rapport by de Lamarck & Cuvier: 7–9. Reprint of Férussac 1812 (Ann. Mus. Hist. natur., **19**: 242–256): 10–22. Partial reprint of Desmarest 1813 (J. Mines, **34** (199): 49–70): 23–30. Rapport by de Lamarck & Cuvier: 31–33].

Furon, R.; Soyer, R. (1947): Catalogue des fossiles tertiaires du bassin de Paris. – Sav. Hist. nat., **22**: 240 pp., 32 pl. Paris (Paul Lechevalier) [is also vol. 6 of "Guides techniques du naturaliste"].

Giusti, F.; Pezzoli, E. (1984): Notulae malacologicae, XXIX: Gli Hydrobiidae salmastri delle acque costiere Italiane: primi cenni sulla sistematica del gruppo e sui caratteri distintivi delle singole morfospecie. – Lav. Soc. ital. Malacol., **21**: 117–148.

Glibert, M. (1962): Les Mesogastropoda fossiles du Cénozoique étranger des collections de l'Institut royal des Sciences naturelles de Belgique. 1e. partie: Cyclophoridae à Stiliferidae (inclus). – Mém. Inst. roy. Sci. natur. Belg., 2me Sér., **69**: 1–305.

Gély, J.-P. (2008): La stratigraphie et la paléogéographie du Lutétien en France. – In: Merle, D. (Coord.): Stratotype Lutétien. – Coll. Patrim. géol., **1**: 76–109.

Hershler, R.; Davis, C.L.; Kitting, C.L.; Liu, H.-P. (2007): Discovery of introduced and cryptogenic cochliopid gastropods in the San Francisco estuary, California. – J. mollusc. Stud., **73** (4): 323–332; correction in J. moll. Stud. **76** (2): 199, V.2010. [received 10.12.2007].

Hershler, R.; Ponder, W.F. (1998): A review of morphological characters of hydrobioid snails. – Smithsonian Contr. Zool., **600**: i–iv, 1–55.

Hershler, R.; Thompson, F.G. (1992): A review of the aquatic gastropod subfamily Cochliopinae (Prosobranchia: Hydrobiidae). – Malacol. Rev., Suppl., **5**: 1–140.

Janssen, R. (2007): Mollusken aus den Mittleren Pechelbronn-Schichten (tiefes Unter-Oligozän) der Bohrungen W07 and B98–BK5 bei Wallau (Hessen). – Geol. Abh. Hessen, **116**: 205–233, Beilage 5.

Kadolsky, D. (1989): Stratigraphie und Molluskenfaunen von „Landschneckenkalk" und „Cerithienschichten" im Mainzer Becken (Oberoligozän bis Untermiozän?). Stratigraphische, paläogeographische und paläoökologische Ergebnisse. – Geol. Jb., Ser. A, **110**: 69–133. [1988 printed in work, but offprints and volume received XII. 1989 by D. Kadolsky; date stamp in GSL copy: 22.1.1990].

Kadolsky, D. (1993): Der Gattung *Nystia* zugeordnete Arten im Tertiär des mittleren und westlichen Europas (Gastropoda: Rissooidea). – Arch. Molluskenkde., **122** (Zilch-Festschrift): 335–402. [28.2.1993].

Kadolsky, D. (2008a): Mollusks from the Late Oligocene of Oberleichtersbach (Rhön Mountains, Germany), Part 2: Gastropoda: Neritimorpha and Caenogastropoda. – Cour. Forsch.-Inst. Senckenberg, **260**: 103–137. [26.6.2008; received 27.7.2008].

Kadolsky, D. (2008b): Zur Identität und Synonymie der häufigeren „Hydrobien" der Rüssingen-Formation (*Inflata*-Schichten) und Wiesbaden-Formation (Hydrobien-Schichten) (Miozän, Mainzer Becken) (Gastropoda, Prosobranchia: Rissooidea). – Senckenbergiana lethaea, **88** (2): 229–266. [offprints received 16.1.2009].

Kadolsky, D. (in press): Proposed suppression of *Paludina conica* Férussac, 1814, with the preservation of *Paludina conica* Prévost, 1821 (currently „*Peringia*“ *conica*) (Gastropoda: Prosobranchia: Hydrobiidae). – Bull. zool. Nomencl., **71** (4).

Koenen, A. v. (1882): Die Gastropoda holostomata und tectibranchiata, Cephalopoda und Pteropoda des Norddeutschen Miocän. – N. Jb. Mineral., Geol. Paläont., Beil.-Bd., **2**: 223–363, pl. 5–7.

Kowalke, T. (1998): Bewertung protoconchmorphologischer Daten basaler Caenogastropoda (Cerithiimorpha und Littorinimorpha) hinsichtlich ihrer Systematik und Evolution von der Kreide bis rezent. – Berliner geowiss. Abh., Ser. E, **27**: 1–121.

Lamarck, J.B.P.A. de (1838): Histoire naturelle des animaux sans vertèbres. Deuxième édition, revue et augmentée de notes présentant les faits nouveaux dont la science n'est enrichie jusqu'à ce jour, **8**: 1–660, Paris (J.B.Baillière).

Le Renard, J. (1997): Clefs de détermination des petites espèces de Gastéropodes de l'Éocène du bassin parisien. XLI– Le genre *Bouryia* Cossmann, 1888 (espèces parisiennes et des bassins de Nantes et du Cotentin). – Cah. Naturalist., Bull. Naturalist. Parisiens, N. S. **51** [pour 1995] (1): 1–34. [VIII. 1997].

Le Renard, J.; Pacaud, J.-M. (1995): Révision des mollusques Paléogènes du bassin de Paris II – Liste des références primaires des espèces. – Cossmanniana, **3** (3): 65–132. [V. 1995].

Liu, H.-P.; Hershler, R.; Thompson, F.G. (2001): Phylogenetic relationships of the Cochliopinae (Rissooidea: Hydrobiidae): an enigmatic group of aquatic Gastropods. – Molec. Phylogenet. Evol., **21** (1): 17–25. [X. 2001].

Mantell, G. (1839): The wonders of geology, **1**: i–xvi, 1–376 + app. + gloss. London (Relfe & Fletcher).

Marcus, E.; DuBois-Reymond Marcus, E. (1963): Mesogastropoden von der Küste São Paulos. – Akad. Wiss. Lit. [Mainz], Abh. math.- naturwiss. Kl., **1963** (1): 1–103. [10.8.1963].

Merle, D. (Coord.; 2008): Stratotype Lutétien. – Coll. Patrim. géol., **1**: 1–288 + CD-ROM.

d'Orbigny, A. (1850): Prodrome de Paléontologie stratigraphique universelle des animaux mollusques et rayonnés faisant suite au course élémentaire de Paléontologie et de Géologie stratigraphique, **2**: 1–422. Paris (Victor Masson).

Pacaud, J.-M. (2008): Mollusca. – In: Merle, D. (Coord.): Le contenu paléontologique du Lutétien du bassin de Paris. – Coll. Patrim. géol., **1**: 40–95 (CD-ROM).

Pacaud, J.-M.; Le Renard, J. (1996): Révision des mollusques paléogènes du bassin de Paris IV – Liste systématique actualisée. – Cossmanniana, **3** (4): 151–187. [„XII. 1995“, but date stamp in BMNH copy: 4.4.1996].

Paladilhe, A. (1874): Monographie du nouveau genre *Peringia* suivie de desciptions d'espèces nouvelles. – Ann. Sci. natur., 6me Sér.: Zool. Paléont., **1** (2): 1–38, pl. 3.

Pallary, P. (1901): Sur les mollusques fossiles terrestres, fluviatiles et saumâtres de l'Algérie. – Mém. Soc. géol. France, Paléont., **9** (22): 1–213, pl. 3–6.

Pilsbry, H.A.; McGinty, T.L. (1949): New marine mollusks of Florida and the Bahamas. – Nautilus, **63** (1): 9–15, pl. 1. [VII. 1949].

Prévost, C. (1821): Sur un nouvel example de la réunion de coquilles marines et de coquilles fluviatiles dans les mèmes couches. – J. Phys. Chim. Hist. natur., **92**: 418–427. [VI.1821].

Sandberger, F. (1870–1875): Die Land- und Süßwasserconchylien der Vorwelt. –1–1000, pl. 1–36. Wiesbaden (Kreidel) [Livr. 1: 1–48, pl. 1–4 , 1870; Livr. 2–3: 49–96, pl. 5–12, 1871 (before 28.3.); Livr. 4–5: 97–160, pl. 13–20, 1871; Livr. 6–8: 161–256, pl. 21–32, 1872; Livr. 9–10: 257–352, pl. 33–36, 1873; Livr. 11: 353–616, 1875; Livr. 12: 617–1000, 1875. Dates according to literature reports in N. Jb. Mineral. Geol. Paläont. 1870–1876; Nachr.-Bl. dt. malakol. Ges., **2** (1870); Verh. k. k. geol. R.-Anst., **6** (1871); written communication by Kreidel to NHMUK]

Schütt, H. (1988): Ergänzungen zur Kenntnis der Molluskenfauna oberpliozäner Süßwasserkonglomerate Syriens. – Arch. Molluskenkde., **118** (4/6): 129–143, pl.1–3. [7.1.1988].

Szarowska, M. (2007): Molecular phylogeny, systematics and morphological character evolution in the Balkan Rissooidea (Caenogastropoda). – Fol. Malacol., **14** (3): 99–168. [31.1. 2007; date stamp NHMUK: 25.7.2007].

van Aartsen, J.J. (2008): The Assimineidae of the Atlantic-Mediterranean seashores. – Basteria, **72** (4–6): 165–181.

Wenz, W. (1923–1930): Gastropoda extramarina tertiaria: Fossilium Catalogus, I: Animalia: (17): 1–352, 20.3.1923; (18): 353–736, 27.4.1923; (20): 737–1068, 5.6.1923; (21): 1069–1420, 2.8.1923; (22): 1421–1734, 9.9.1923; (23): 1735–1862, 20.11.1923; (32): 1863–2230, 26.2.1926; (38): 2231–2502, 28.7.1928; (40): 2503–2886, 4.2.1929; (43): 2887–3014, 8.7.1929; (46): 3015–3387, 10.4.1930; Berlin (W. Junk).

Wilke, T.; Haase, M.; Hershler, R.; Liu, H.-P.; Misof, B.; Ponder, W. (2012): Pushing short DNA fragments to the limit: phylogenetic relationships of 'hydrobioid' gastropods (Caenogastropoda: Rissooidea). – Molec. Phylogenet. Evol., **66**: 715–736. [available online 7.11.2012].

Wilke, T.; Davis, G. M.; Falniowski, A.; Giusti, F.; Bodon, M.; Szarowska, M. (2001): Molecular systematics of Hydrobiidae (Mollusca: Gastropoda: Rissooidea): testing monophyly and phylogenetic relationships. – Proc. Acad. natur. Sci. Philadelphia, **151**: 1–21. [31.12.2001].

Wilke, T.; Davis, G. M.; Gong, X.; Liu, H.-X. (2000): *Erhaia* (Gastropoda: Rissooidea): phylogenetic relationships and the question of *Paragonimus* coevolution in Asia. – Amer. J. trop. Med. Hyg., **62** (4): 453–459.