# Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 21<sup>1</sup>. Early and Middle Eocene (Ypresian-Lutetian) holoplanktonic Mollusca (Gastropoda) from Uzbekistan

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Six samples from two localities in Eocene deposits of central Uzbekistan yielded 14 species of holoplanktonic molluscs (1 Pterotracheoidea, 9 Limacinoidea, 3 Cavolinioidea and 1 Cymbulioidea). *Limacina asiatica* spec. nov. and *L. dzheroiensis* spec. nov. are introduced. The assemblages are interpreted as belonging to the later part of Pteropod Zone 9 (Ypresian, two samples) and the early part of Zone 10 (Ypresian-Lutetian, four samples) and correlated with the existing global nannoplankton zonation (zones NP 13 to lower NP 15).

Key words: Gastropoda, Pterotracheoidea, Limacinoidea, Cavolinioidea, Cymbulioidea, taxonomy, biostratigraphy, Eocene, Uzbekistan.

#### INTRODUCTION (BY C. KING)

This publication deals with Early and Middle Eocene holoplanktonic molluscs (Gastropoda, Pterotracheoidea and Thecosomata) obtained from thin phosphatic beds exposed at two sites in central Uzbekistan.

Note: Uzbekistan was formerly part of the Soviet Union; during this period Cyrillic transliterations of geographic names were used. Since 1995 Uzbek has been the official language and the Roman alphabet has been adopted. This has resulted in changes to almost all former names; here both current and former names are cited where necessary, as the Soviet-era names are used in most previous literature and maps.

#### STRATIGRAPHY (BY C. KING)

Eocene sediments crop out extensively in central Uzbekistan in the Qizilqum (Kyzyl Kum) desert (Fig. 1). The major lithostratigraphic units are consistent throughout this area.

<sup>1</sup> For nr 20 in this series see Basteria 72: 159.

There is no adequate English-language description of the succession. Summaries are given by Morozov et al. (1988), Dalimov et al. (1998) and Zhelezhko & Kozlov (1999). A more detailed account is given by Mirkamalova (1958). The Ypresian and Lutetian are represented by the Suzak, Alay and Turkestan 'horizons', here regarded as formations.

The fossils described herein are from the Alay Formation and the basal Turkestan Formation. In the area dealt with here, the Suzak Formation (mid Ypresian, nannoplankton zone NP11) comprises non-calcareous and calcareous clay. The Alay Formation (mid-late Ypresian, NP12-NP14) comprises dominantly chalk and marl, with microfaunas indicating mid to outer neritic environments. Planktonic foraminiferids are relatively common at most levels. The Turkestan Formation (Lutetian) comprises mainly non-calcareous or weakly calcareous clays, although the lower part is calcareous in some areas. The lower part contains microfaunas indicating a mid-neritic environment, with common planktonic foraminiferids. Its contact with the Alay Formation is an interburrowed omission surface, with phosphate concentrated at the base in some areas.

MATERIAL AND METHODS (BY C. KING)

Fossils were obtained from two sections, c. 60 km apart, near the town of Zarafshon (Zarafshan) (Figs 1, 2). These were logged and sampled by CK in 2003 and 2004.

## Dzheroi (Jeroy) (N 41°38′58″, E 064°39′50″).

The locality name 'Dzheroi 1' was initially used by Nessov et al. (1987) for a small temporary exposure 32 km ESE of the section at approximately 41° 32′ 40″ N 65° 1′ 30″ E, probably in the Alay Formation. The term 'Dzheroi 2′ is a locality name applied to a small vertebrate-rich sand quarry at a higher stratigraphic level (probably Bartonian: Averianov, 1997) 2.2 km E of the described section.. This site was referred to as 'near Actau Mountain' by Case et al. (1996).

The site described here is a small ravine in which the Suzak, Alay and lower Turkestan Formations are exposed. The Suzak Formation overlies Palaeozoic basement. The Suzak Formation (2.4 m) and Alay Formation (5.0 m) are relatively thin. Two thin phosphatic levels (D1 and D2) were



**Fig. 1**. General map of Uzbekistan, with location of the Dzheroi (Jeroy) and Tashkura localities.

sampled. Pteropods were isolated from sieving residues of three samples:

D1 – 1 m below the top of the Alay Formation (sample UZ 260): a lenticular unit (max. c. 0.10 m) of marl packed with granule-size phosphate pellets, many of which are phosphatised faecal pellets. The base is probably a burrowed omission surface. Phosphatised pteropods are abundant, preserved as internal moulds, often slightly abraded, together with some small benthic molluscs.

D2 – The basal 0.1 m of the Turkestan Formation (samples UZ 250B and UZ 262). The lowest 0.25 m of the Turkestan Formation is a highly weathered and oxidised unit, with abundant secondary gypsum, probably originally a sandy marl. Pelletal phosphate is abundant in the lowest 0.1 m, with occasional phosphatic pebbles and some quartz granules. The base is sharp, with thalassinoid burrows penetrating the topmost Alay Formation. Phosphatised pteropods are abundant, together with phosphatised and unphosphatised foraminiferids and ostracods. Some small phosphatised bivalves and benthic gastropods also occur. Planktonic foraminiferids are common.

# Tashkura (approximately N 41°13'50", E 064°12'18")

A phosphate quarry in which the upper Alay Formation and basal Turkestan Formation are exposed. Due to the method of excavation exposures were poor, and it was not



**Fig. 2**. Stratigraphy of the Dzheroi (Jeroy) and Tashkura sections, and position of samples. T and D represent phosphatic levels.

possible to log a continuous section. Pteropods were picked from decantation residues of sediment samples from three thin phosphatic levels in the Alay Formation, referred to as T1 to T3:

T1 – Sample UZ 405. at 1.05 m below level T2.

T2 – Sample UZ 404. Stated to be c. 9 m below level T3, but this could not be confirmed.

T3 – Sample UZ 406. A very diffuse thin phosphatic layer c. 1.0 m below the base of the Turkestan Formation. This is probably the same as layer D1 at Dzheroi.

T4 –This phosphatic level, at the base of the Turkestan Formation, was not sampled.

Both these sites are adjacent to the Palaeozoic massif of Tamditau, onto which the Eocene oversteps the Cretaceous. It is possible that this may have been a 'high' during the Early and early Middle Eocene, with development of phosphatic beds in this area reflecting reduced sedimentation or possibly episodes of uplift. All specimens are in phosphoritic preservation, frequently in the form of internal moulds, but in many specimens the actual shell is phosphatised as well. In spite of the fact that reworking for the present samples most probably is not important, many specimens look as if they have been transported or as if they are covered with a patina, making shell details like suture, umbilicus or protoconch difficult to discern. Specimens from Dzheroi are generally brownish to rusty in colour and frequently preserved as internal moulds, whereas in the Tashkura material most of them are whitish with their shells still present.

Abbreviations: NHMUK (formerly BMNH), The Natural History Museum, London, UK; RGM, Netherlands Centre for Biodiversity Naturalis, Leiden, The Netherlands (Palaeontology department), formerly Rijksmuseum van Geologie en Mineralogie; FOD, first occurrence datum; H, shell height; W, shell width; H/W, height/width ratio = H/W x 100; LOD, last occurrence datum.

# CALCAREOUS NANNOPLANKTON ZONATION (BY E. STEURBAUT)

The calcareous nannofossil investigation is based on a thorough study of seven samples from the Alay Formation, and two samples from the Turkestan Formation in the Dzheroi section (Fig. 2). The lower Dzheroi sample was taken at 1 m above phosphorite level D2 (UZ 252), the upper at the top of the section (UZ 256). Calcareous nannofossils are fairly common, although moderately to strongly dissolved, and presenting clear, but varying degrees of recrystallization. As a consequence, the associations are clearly biased in most of the samples in favour of the most solid forms. However, most of the marker species identified in the late 1980s and early 1990s in the North Sea Basin (essentially Belgium: Steurbaut & Nolf, 1989; Steurbaut, 1986,1990,1991; Smith et al., 2004) and recently at Aktulagay, western Kazakhstan (King et al., in prep.), are recognized in the Uzbekistan sections studied here, allowing high-resolution dating. The taxonomy is essentially from Perch-Nielsen (1985), taking into account the subsequent modifications by Varol (1992) and Aubry & Bord (2009).

The samples from the lower part of the Alay Formation,

beneath phosphatic level T3 and its equivalent D1, are fairly similar and marked by *Discoaster cruciformis*, *D. lodoensis*, *Ectalithus crassus*, *Nannoturba robusta*, *N. spinosa*, *Helicosphaera seminulum*, *Blackites creber* and *Cruciplacolithus mutatus*. The co-occurrence of these species, associated with the absence of *Tribrachiatus orthostylus*, *Helicosphaera lophota* and *Chiphragmalithus acanthodes*, indicates the middle part of Martini's (1971) standard nannoplankton zone NP13.

The association of level T3 (UZ 406) is similar to that of D1 (UZ 260), although much better preserved. It includes a few typical 5-rayed *Discoaster sublodoensis*, typical *D. lodoensis* and a whole series of transitional forms (such as *D. strictus* and others), as well as *C. acanthodes*, *Cyclococcolithus* spec. and rare *Pemma* spp. The samples from the top of the Alay Formation (UZ 261 and UZ 253) are identical to these of T3 and D1, although include a much higher number of *D. sublodoensis*, indicating a slightly younger age. The absence of *Blackites inflatus* indicates that the topmost meter of the Alay Formation, including its upper phosphatic horizon T3-D1, belongs to the lower part of NP 14 (NP 14a according to Berggren & Pearson, 2005).

The base of the Lutetian has in the past been defined at the FOD of the planktic foraminiferid *Hantkenina* at c. 48.6 Ma (e.g. Luterbacher et al., 2004), corresponding approximately to the base of NP14, but recent studies have shown this event to be significantly diachronous. The Gorrondatxe section (NW Spain) was recently proposed as a candidate stratotype for the Ypresian/Lutetian boundary (Orue-Extebarria et al., 2006). A GSSP, corresponding to the FOD of *Blackites inflatus* (base of NP14b), was approved by the International Commission on Stratigraphy in early 2011, and finally ratified by the International Union of Geological Sciences in April 2011 (Molina et al., 2011). This definition is adopted here.

The lowermost sample of the Turkestan Formation (UZ 252) presents a fairly rich, moderately to well-preserved assemblage in which medium-sized Prinsiaceae dominate. The records of *Nannotetrina quadrata*, *Nannotetrina* spec. and *Blackites inflatus* point to the lower part of NP 15, although not the extreme base. These species do not range up the topmost sample of the Dzheroi section (UZ 256). The latter can be assigned to the combined interval middle/upper NP 15 - NP 16, because of the co-occurrences of *Dictyococcites callidus*, *Chiasmolithus solitus* and *Clausicoccus fenestratus*.

From the foregoing it is clear that the boundary between the Alay Formation and the Turkestan Formation corresponds to a substantial hiatus of which the duration is estimated at approximately 1.3 m.y. (absence of NP 14b; time according to Berggren & Pearson, 2005). There is also a minor break in sedimentation at level D1, within the upper part of the Alay Formation. This period of non-deposition is unlikely to have persisted for more than a few 100 k.y.

# Systematic part (by A.W. Janssen)

Note. – Lists of synonyms are mainly restricted to the first valid description and to some selected papers, in which a species is well-described and/or -illustrated. Descriptions of well-known species are usually omitted, the reader is referred to one or more of the recent publications given in the synonyms.

Systematics above genus level are according to Janssen (2003) and Bouchet & Rocroi (2005). To prevent the impression that the present author has a pronounced opinion on higher classification only ranks of superfamily and lower are given here.

Pterotracheoidea Rafinesque, 1814; Pterotracheidae Rafinesque, 1814

# Pterotrachea Forskål, 1775.

Type species (by monotypy): Pterotrachea coronata Forskål, 1775 (Recent).

# Pterotrachea spec. (Figs 3-6)

Description. – Very small, dextral, almost planorboid gastropod, about twice as wide as high (largest specimen: H = 0.44 mm, W = 0.90 mm), of c. 1½ whorls with a circular transverse section. The ultimate half whorl separates from the preceding one. The relatively large aperture is circular without any reinforcement structures and forms the entire height of the shell, its basal part lowered beyond the base of the previous whorl. The shell is widely umbilicated.



**Figs 3-8**. *Pterotrachea* spec. **3**, RGM 570 769, Dzheroi UZ 250B; **4-6**, RGM 570 771a-c, Dzheroi UZ 260 (Eocene); **7-8**, RGM 569 104a-b, Eastern Mediterranean, S of Crete, gravity core T87/2/20G, 2.42-2.43 m below sea bottom (Pleistocene, Eemian). Bar 100 μm.

Material examined. – RGM 570 769/1 (Fig. 3a-b), Dzheroi UZ 250B; RGM570 770/4, RGM 570 771a-c/3 (Figs 4-6), Dzheroi UZ 260.

Discussion. – The specimens strongly resemble the larval shells of Late-Quaternary to Recent *Pterotrachea* spec., as described by Krohn (1860: 312, pl. 2 fig. 22), Richter (1968: 373, fig. 19), Thiriot-Quiévreux (1969: 355, pl. 4 fig. 5) and Seapy (2008, Tree of Life website, 5 figs). The only differences seem to be that the Recent species remains somewhat smaller and has ½ to ¼ whorl less. The resemblance, however, of overall shell shape and the separation of the last part of the body whorl are virtually identical. Furthermore, their occurrence

in an assemblage of predominantly holoplanktonic species renders the occurrence of pterotracheids not unlikely.

Recent species of *Pterotrachea* have no shell in the adult stage. The minute larval shells, three different Recent species of which are described in literature, are shed at metamorphosis of the larva to adult individual and cannot yet be identified as belonging to one of the known living species. The present specimens resemble most the type indicated as *Pterotrachea* Larva 1 by Richter (1968), who supposed it to belong to the species *P. hippocampus* Philippi, 1836. Two Pleistocene specimens of this type are illustrated in Figs 7 and 8. The genus *Pterotrachea* was already recorded from the Jurassic of southern Germany by Bandel & Hemleben (1987), who described a species, *P. liassica* Bandel & Hemleben, 1987, strongly resembling one of the Recent species of this genus, showing distinct radial ornament, identified by these authors as *P. coronata* Forskål, 1775.

Limacinoidea Gray, 1847; Limacinidae Gray, 1847

*Altaspiratella* Korobkov, 1966. Type species (by original designation): *'Limacina elongatoides'* (Aldrich)' = *Physa elongatoidea* Aldrich, 1887 (Eocene, Ypresian).

Altaspiratella multispira (Curry, 1982) (Figs 9-12) Plotophysops multispira Curry, 1982: 42, pl. 1 fig. 10 a-c. Altaspiratella multispira; Cahuzac & Janssen, 2010: 27, pl. 2 figs 6-10.

Description. – See Curry (1982) and Cahuzac & Janssen (2010).

Material examined. – RGM 570 772/11, RGM 570 773a-c/3 (Figs 10a-c, 11, 12), Dzheroi UZ 260; RGM 570 774/1, RGM 570 775/1 (Fig. 9a-c), Dzheroi UZ 262; RGM 570 776/1, Tashkura UZ 406.

Discussion. – Although generally in rather poor preservation the available specimens are easily recognisable as belonging to this species. It is the only known limacinid in which both the adult shell as well as the individual whorls are so high in shape. The interesting apertural structures of



**Figs 9-12**. *Altaspiratella multispira* (Curry, 1982). **9**, RGM 570 774, Dzheroi UZ 262; **10-12**, RGM 570 773a-c, Dzheroi UZ 260 (Eocene). Bar 100 μm.

this species are in the present material not preserved. So far, *Altaspiratella multispira* was known only from the Ypresian marls of Gan (SW France).

## Heliconoides d'Orbigny, 1834.

Type species (by subsequent designation of Herrmannsen, 1846: 514): Atlanta (Heliconoides) inflata d'Orbigny, 1834 (Recent).

Heliconoides mercinensis (Watelet & Lefèvre, 1885) (Figs 13-16) Spirialis mercinensis Watelet & Lefèvre, 1885: 102, pl. 5 fig. 2a-c. Spiratella mercinensis; Curry, 1965: 366, figs 15, 16.

*Heliconoides mercinensis*; Janssen et al., 2007: 163, figs 7-8 (with extensive synonymy); Janssen, 2010: 165, fig. 2; Cahuzac & Janssen, 2010: 41, pl. 9 fig. 1a-b.

Description. – See Curry (1965), Cahuzac & Janssen (2010). Shell very small (specimen illustrated Fig. 13: H = 425  $\mu$ m, W = 630  $\mu$ m), consisting of up to 3 convex whorls, gradually increasing in diameter. In a large, but poorly preserved specimen (Fig. 16) with a diameter of 1.2 mm the basal part of the apertural margin is preserved. Sutures are clear in well-preserved specimens, but usually visible only with difficulty in



**Figs 13-16**. *Heliconoides mercinensis* (Watelet & Lefèvre, 1885). **13-14**, RGM 570 778a-b; **15**, RGM 570 781, Tashkura UZ 405 (Eocene); **16**, RGM 570 779, Tashkura UZ 404. Bar 100 μm.

the present material. The apical plane of the shell is almost completely flat or very slightly concave. The aperture is large, almost circular. There is a distinct umbilicus, which in almost all specimens is concealed by matrix.

Material examined. – RGM 570 777/many, RGM 570 778a-b/2 (Figs 13, 14), RGM 570 779/1 (Fig. 16), Tashkura UZ 404; RGM 570 780/many, RGM 570 781/1 (Fig. 15), Tashkura UZ 405; RGM 570 782/many, Tashkura UZ 406. Alltogether several hundreds of mainly juvenile specimens are available.

Discussion. – In spite of the fact that the characteristic apertural structures of this species are retained in just a single specimen I consider the identification satisfactory, after comparison of the present material with juvenile specimens from the Ypresian of the Paris Basin. *Heliconoides pyrenaica* Janssen, in Cahuzac & Janssen, 2010, exclusively known



**Figs 17-18**. *Heliconoides* spp. **17**, *Heliconoides* aff. *paula* (Curry, 1982), RGM 570 784, Tashkura UZ 404 99 (a: frontal, b: lateral views) (Eocene); **18**, *H. paula* (Curry, 1982), NHMUK GG 21251, Gan (SW France), after Cahuzac & Janssen (2010, pl. 9 fig. 6) (Eocene, Ypresian, Marnes de Gan). Bar 100 μm.

from the Ypresian of Gan (SW France) has a similar shape but with a relative higher H/W-ratio (compare pl. 3, fig. 4 in Cahuzac & Janssen, 2010). The generally unfavourable preservation of the specimens prevents to decide with certainty if juvenile specimens of *H. pyrenaica* might be among them.

Heliconoides aff. paula (Curry, 1982) (Fig. 17) Spiratella paula n. spec.; Curry, 1982: 38, pl. 1 fig. 6a-b. Heliconoides paula (Curry, 1982); Cahuzac & Janssen, 2010: 40, pl. 3 fig. 2; pl. 9 fig. 6.

Description. – Some of the smallest specimens in the Tashkura sample UZ 404 do not agree with any of the other Uzbekistan limacinids. The largest among them reaches a shell height of 0.75 mm only and is about as hight as wide. The apex is damaged but presumably there are somewhat more than four whorls. The aperture is semicircular and there are no apertural reinforcements preserved. The tangents along the whorls are slightly convex. A narrow umbilicus is indicated but covered with matrix.

Material examined. – RGM 570 783/4, RGM 570 784/1 (Fig. 17a-b), Tashkura UZ 404.

Discussion. – In size and general shape these few specimens resemble *Heliconoides paula*, a species thus far exclusively known from the Ypresian of Gan (SW France, see Curry, 1982: 38, pl. 1, fig. 6a-b; Cahuzac & Janssen, 2010: 40, pl. 3, fig. 2; pl. 9, fig. 6). The holotype of that species is reproduced here in Fig. 18 for comparison. The Tashkura specimens, however, reach slightly larger dimensions and are more globose, with a somewhat wider apical angle, and apertural reinforcements are not present or not preserved. Therefore I choose to indicate these specimens in open nomenclature.

# *Limacina* Bosc, 1817 Type species (by monotypy): *Clio helicina* Phipps, 1774 (Recent)

*Limacina asiatica* Janssen spec. nov. (Figs 19-23) *Limacina* spec. 1; Ando et al. 2009: 189, pl. 4 fig.5a-b. Limacinidae spec. 2; Cahuzac & Janssen, 2010: 51, pl. 13 fig. 6.

Type series. – Holotype: RGM 570 790, Dzheroi UZ 262 (H = 0.94 mm, W = 1.20 mm (Fig. 19). Paratypes: RGM 570 785/many, Dzheroi UZ 250B; RGM 570 786/many, RGM 570787/1 (Fig. 22), Dzheroi UZ 260; RGM 570 788/many, RGM 570 789a-b/2 (Figs 20-21), Dzheroi UZ 262; RGM 570 791/many, Tashkura UZ 406, (Eocene); RGM 396 609/1 damaged specimen (Fig. 22, after Cahuzac & Janssen, 2010, pl. 13, fig. 6), Gan (France, Pyrénées Atlantiques) (Eocene, Ypresian, Marnes de Gan).

Etymology. - Named after the continent of Asia.

Diagnosis. – *Limacina* of average dimensions (holotype W = 1.2 mm) and 3<sup>3</sup>/<sub>4</sub> whorls, with a but slightly elevated spire, H/W-ratio 73-82 (holotype 78.3). Body whorl comparatively large. Aperture circular, base perforate.

Description. – Rather low-spired *Limacina* species of 3<sup>3</sup>/<sub>4</sub> moderately convex whorls, regularly increasing in diameter. Body whorl large and convex, somewhat swollen, occupying almost the entire shell height. Aperture large, circular, occupying approximately three quarters of the shell height, slightly indented by the preceding whorl, apertural margin not reinforced, lower margin protruding beyond the base of the penultimate whorl. Base of the body whorl evenly convex and umbilicated. Umbilicus covered with matrix in virtually all available specimens. H/W-ratio of holotype is 78.3, variable in the paratypic material between c. 73 and 82. Discussion. – The single specimen from the Ypresian of Gan, 77





indicated as Limacinidae spec. 2 from Gan (SW France) in Cahuzac & Janssen (2010), reillustrated here as Fig. 21, undoubtedly represents the same species.

*Limacina augustana* (Gardner, 1951) (see Hodgkinson et al., 1992: 15, pl. 2, figs 1-3), from the Ypresian/Lutetian Tallahatta Formation of Alabama (USA) seems to be closely related but remains distinctly lower to almost planorboid and reaches far larger dimensions (holotype 2.6 mm). On the other hand *L. asiatica* is similar to low-spired forms of the Late-Oligocene to Miocene *Limacina valvatina* (Reuss, 1867), e.g. its Late-Miocene forma *weinbrechti* (Tembrock, 1989) in which, however, the spire always occupies a more substantial part of the shell's height. Of course, there also is the considerable difference in age.

*Limacina* spec. 1, a single specimen recorded by Ando et al. (2009) from the Shiklyama Formation (nannoplankton zone CP 13 = NP 15), of the Amakusa region in Japan, resembles the present species closely, its age was indicated as Middle Eocene. A direct comparison would be necessary for a certain identification.

Limacina dzheroiensis Janssen spec. nov. (Figs 24-29)

? Spiratella pygmaea (Lamarck, 1804); Curry, 1965: 362, fig. 18a-b [only (part of ?) the specimens from UK] (non Lamarck?).

Type series. – Holotype RGM 570 796 (Fig. 22), Dzheroi UZ 262. Paratypes: RGM 570 792/1, Dzheroi UZ 250B; RGM 570 793/19, Dzheroi UZ 260; RGM 570 794/5, RGM 570 795a-c/3 (Figs 23-25), Dzheroi UZ 262; RGM 570 797/1, RGM 570 798a-b/2 (Figs 26-27), Tashkura UZ 406.

Etymology. – Named after the type locality.

Diagnosis. – Small limacinid of regular, naticoid shape, just slightly wider than high, with a low spire of  $3\frac{1}{2}$  convex whorls, separated by distinct sutures. Base rounded, umbilicate. Description. – Sinistral, reversed naticiform shell, slightly wider than high (holotype H = 0.82 mm, W = 0.88 mm, a few damaged specimens reach somewhat larger dimensions), of c.  $3\frac{1}{2}$ -4 convex whorls, gradually and rather rapidly increasing in diameter, separated by incised sutures. The body whorl is globose, the aperture lunate and relatively large, occupying slightly more than  $\frac{3}{4}$  of the entire shell height, with a gradually curved abaxial margin. There are no apertural reinforcements. The base of the shell is regularly rounded,



Figs 24-29. *Limacina dzheroiensis* spec. nov., holotype and paratypes. 24, holotype, RGM 570 796, Dzheroi UZ 262; 25-27, RGM 570 795a-c, Dzheroi UZ 262; 28-29, RGM 570 798a-b, Tashkura UZ 406 (Eocene). Bar 100 μm.

the presence of an umbilicus is obvious, but it is usually obscured by matrix.

Discussion. – This species differs from the co-occurring *Limacina pygmaea* by its relatively wider shape, less pronounced body whorl and commonly more developed apical shell part with convex whorls. Among the many less favourably preserved specimens of these species, however, it is sometimes difficult to assign a specimen to one species or the other.

Specimens recorded by Curry (1965: 362, fig. 18a-b) from 'Fisher Bed 1', Lower Bracklesham Beds (upper part, Lutetian) at Bracklesham Bay (Sussex, UK) were identified as *Spiratella pygmaea* (Lamarck), but at least the illustrated specimen is unlike the Paris Basin ones of this species in having a more naticoid shell, similar to the new species described here. More specimens will be needed before declaring them identical with the Uzbekistan species. No similar occurrences elsewhere in the North Sea Basin are known to me.

*Limacina erasmiana* Janssen, 2010 (Figs 30-35) *Limacina erasmiana* spec. nov.; Janssen, 2010: 166, figs 3-6.

Description. – Sinistral, high-conical shell, when complete and fully grown with  $5\frac{3}{4}$  convex whorls and c. 1.35 times higher than wide, with straight tangents and an apical angle of c. 40°. The initial  $1\frac{1}{2}$  whorls are planispiral (Fig. 31) resulting in a blunt apex. The aperture is relatively small and cir-



Figs 30-35. Limacina erasmiana Janssen, 2010. 30-34, RGM 570 800a-e, Tashkura UZ 404; 35, RGM 570 802, Tashkura UZ 405 (Eocene). Bar 100 μm.

cular, positioned slightly oblique with respect to the shell's long axis, occupying four tenths of the adult shell height. There are no apertural reinforcements. A narrow umbilicus is present.

Material examined. – RGM 570 799/many (mainly juveniles), RGM 570 800a-e/5 (Figs 30-34), Tashkura UZ 404; RGM 570 801/50 juveniles, RGM 570 802/1 (Fig. 35), Tashkura UZ 405.

Discussion. – The holotype (Janssen, 2010, fig. 3a-c) from the Ypresian of Rotterdam (The Netherlands) is the only fully grown and well-preserved specimen. Its measurements are H 1.32 mm, W 0.98 mm. The predominantly juvenile and rather poorly preserved Tashkura specimens are recognisable by their high conical shape unlike any other *Limacina* species. There are some slight differences with the type lot, as for instance the somewhat more variable, slightly convex or slightly concave tangents along the whorls (compare Figs 34 and 35) and their initial whorl is not so strongly produced.

The occurrence of this species in the Uzbekistan material is very surprising. It was only recently described from the North Sea Basin and is known from just one borehole. This once more demonstrates how little is known so far about the palaeogeography of fossil pteropods. Interestingly, this species was also recognized in some Ypresian samples from Kazakhstan (King et al., MS in preparation).

Limacina pygmaea (Lamarck, 1805) (Figs 36-40)



Figs 36-40. Limacina pygmaea (Lamarck, 1805). 36-38, RGM 570 805a-c, Dzheroi UZ 250b; 39, RGM 570 810, Tashkura UZ 406; 40, RGM 570 808, Dzheroi UZ 262 (Eocene). Bar 100 µm.

Ampullaria (pygmaea); Lamarck, 1805: 30.

Ampullaria pygmaea; Lamarck, 1806, pl. 61 fig. 6a, b.

- ? Spiratella pseudopygmaea n.spec.; Eames, 1952: 160, pl. 6 fig. 146a, b.
- ? Spiratella pygmaea (Lamarck), 1804; Curry, 1965: 362, fig. 18a-b (= Limacina dzheroiensis?)

Spiratella pygmaea (Lamarck); Curry, 1982: 37, pl. 1 fig. 3a, b.

Limacina pygmaea (Lamarck, 1805)?; Janssen et al., 2007: 165, fig. 11.

Limacina pygmaea (Lamarck, 1805); Cahuzac & Janssen, 2010: 46, pl. 12 figs 3-5 (with extensive synonymy).

Description. - Shell small (largest specimen in the present material H = 1.52 mm), sinistral, slightly wider than high to somewhat higher than wide. There are about four whorls in a regular spiral, the apical part of which may be flattened (Figs 36-38), hardly or not visible in a frontal view, or slightly elevated (Fig. 39). Aperture semicircular to obliquely elliptical, apertural margin not reinforced, a columellar thickening is present in this species but hardly or not visible in the available Uzbekistan specimens. Umbilicus narrow,

occupying one seventh of the shell's diameter, but in the Uzbekistan specimens usually covered by matrix.

Material examined. - RGM 570 803/many, RGM 570 805a-c/3 (Figs 36-38), Dzheroi UZ250B; RGM 570 806/many, Dzheroi UZ 260; RGM 570 807/many, RGM 570 808/1 (Fig. 40), Dzheroi UZ 262; RGM 570 809/many, RGM 570 810/1 (Fig. 39), Tashkura UZ 406.

Discussion. - Spiratella pseudopygmaea Eames, 1952 seems to be a juvenile form (H = 0.5 mm) of the present species. The differences mentioned by Eames all fall within the natural variability of the species. A final check on the type material would be necessary. See also the remarks on Spiratella pygmaea, as illustrated by Curry (1965), in the discussion of Limacina dzheroiensis above.

*Limacina* cf. *smithvillensis* Hodgkinson, 1992 (Fig. 41) ?Limacina smithvillensis Hodgkinson, new species; Hodgkinson in Hodgkinson et al., 1992: 19, pl. 3 fig. 16.

Description. - In two of the Dzheroi samples a number of limacinids are represented, practically all of them in a very poor state of preservation, showing an elevated spire, most of them resembling the species Limacina smithvillensis Hodgkinson, introduced from the Viesca Member of the



Fig. 41. Limacina cf. smithvillensis Hodgkinson, 1992; RGM 570 812, Dzheroi UZ 260 (Eocene). Bar 500 µm.



Figs 42-50. *Limacina vegrandis* Janssen, 2010. 42-43, RGM 570 818a-b, Tashkura UZ 404; 44-47, RGM 570 815a-d, Dzheroi UZ 260; 48-49, Paratypes, RGM 541 533, RGM 569 458, Gan, SW France (Eocene, Ypresian); 50, holotype, RGM 396 598, same locality. Bar 100 μm.

Weches Formation (Lutetian) in Texas (USA). The specimen illustrated here (Fig. 41) has similar proportions to the holo-type of *L. smithvillensis*, but among the remaining specimens more slender as well as more thick-set forms are present, together representing a considerable variability.

Material examined. - RGM 570 811/80, RGM 570 812/1 (Fig. 41), Dzheroi

UZ 260; RGM 570 804/8, Dzheroi UZ 262.

Discussion. – Since of *Limacina smithvillensis* just five specimens are known, of which only the holotype was illustrated, it remains unclear if all material from Uzbekistan may be identified with that species. Also, because of the poor preservation, I think it necessary to add a query to the name. It might very well be that the Dzheroi samples represent more than a single taxon.

*Limacina vegrandis* Janssen, 2010 (Figs 42-50) *Limacina? vegrandis* spec. nov; Janssen, in Cahuzac & Janssen, 2010: 49, pl. 11 figs 2-5; pl. 12, fig. 13.

Description. – Shell sinistral, extremely small (height c. 0.35 mm only). H/W ratio in the present material rather variable (compare Figs 40 and 42). There are just 1¼ whorls that increase rapidly in diameter and especially in height; the inflated body whorl equals almost total shell height. Suture in most specimens indistinct. Aperture large and circular, occupying 9/10th of total shell height, with a very concave columellar side. Apertural margin not reinforced, obliquely situated (lateral view). Base gradually rounded and with a very narrow umbilicus, which in the Uzbekistan specimens is always covered with matrix. Very weak subsutural crests are present in some specimens on the upper side of the last half whorl.

Material examined. – RGM 570 813/10, Dzheroi UZ 250B; RGM 570 814/14, RGM 570 815a-d/4 (Figs 44-47), Dzheroi UZ 260; RGM 570 816/1, Dzheroi UZ 262/1; RGM 570 817/56, RGM 570 818a-b/2 (Figs 42-43), Tashkura UZ 404; RGM 570 819/24, Tashkura UZ 405; RGM 570 820/15, Tashkura UZ 406.

Discussion. – The variability among the present specimens is somewhat wider than in the relatively few specimens from Gan (SW France), especially so in H/W-ratio (compare Figs 42 and 44) which in general is slightly lower than in the Gan specimens (holotype and two paratypes from Gan are reillustrated here in Figs 48-50). Still, the overall appearance agrees so strongly with the French specimens that I consider them conspecific. The abundant occurrence of this only very recently discovered and described species is surprising. Superfamily Cavolinioidea Gray, 1850 Family Creseidae Rampal, 1973

Note. – Bouchet & Rocroi (2005: 57, 259), as well as Janssen (2006: 68), considered Curry (1982) to be the author of Creseidae. Curry attributed the authorship of the family to Rampal (1975), which reference, however, was based on an unpublished PhD. The family name was nonetheless already introduced in Rampal (1973), as Creseiidae (see also Janssen & Zorn, 1993).

## Camptoceratops Wenz, 1923

Type species (by original designation): *Camptoceratops prisca* (Godwin-Austen) (Eocene, Ypresian).

Camptoceratops priscus (Godwin-Austen, 1882) (Figs 51-59) Camptoceras priscum Godwin-Austen n. spec.; Godwin-Austen, 1882: 220 pl. 5, figs 1-5.

*Camptoceras priscum* Godwin-Austen var. *obtusum;* Godwin-Austen, 1882: 220, pl. 5 figs 6, 7.

*Camptoceratops prisca* (Godwin-Austen); Curry, 1965: 360, figs 7-10, pls 16, 17.

*Camptoceratops americanus* Garvie, new species; Garvie in Hodgkinson et al., 1992: 25, pl. 7 figs 13-15.

*Camptoceratops priscus* (Godwin-Austen, 1882); Janssen, 2010: 172, figs 15-17; Cahuzac & Janssen, 2010: 52, pl. 5 figs 4-6 52, pl. 13, figs 7-15 (with extensive synonymy).

Description. – See Curry (1965); Cahuzac & Janssen (2010). In the present material in shell preservation from Tashkura a number of specimens (Figs 54-56) retain their slightly swollen protoconch. It is interesting to see that in specimens in internal mould preservation the protoconch looks more accentuated (Fig. 57).

Material examined. – RGM 570 821/many, RGM 570 822/c. 60 retaining protoconch, RGM 570 823a-g/7 (Figs 51-57), Tashkura UZ 404; RGM 570 824/47, Tashkura UZ 405.



Basteria 75 (4-6)

Discussion. – Janssen (in Cahuzac & Janssen, 2010: 53) considered *Camptoceratops americanus* Garvie, in Hodgkinson et al., 1992 (p. 25, pl. 7, fig. 13-15), described from the North American Early Eocene Reklaw Formation, to be a junior synonym of *C. priscus*. The concordance of these taxa is acknowledged by two topotypical paratypes of *C. americanus* in coll. RGM 429 745a-b (Figs 58, 59) (donated C. Garvie, March 2001).

### Euchilotheca Fischer, 1882

Type species (by original diagnosis): *Cleodora Parisiensis* Deshayes [= *Euchilotheca succincta* (Defrance, 1828)] (Eocene, Lutetian).

#### Euchilotheca elegans Harris, 1894 (Figs 60-79)

Siphonodentalium breve, Deshayes, 1861; Newton, 1891: 287 (non Gadus brevis Deshayes, 1861).

*Euchilotheca elegans*; Harris, 1894: 61, fig.; Wrigley, 1934: 10; Curry, 1965: 360, figs 1, 2a-b.

Description. – See Curry (1965). The abundant available specimens are predominantly fragmentary. The thickened apertural margin, as described by Curry (1965), is preserved only in some fragments (see Discussion). The largest more or less complete specimen reaches a height of just over 6 mm. The shell of this species is not straight, but shows a weak flexure.

The larval shell of *Euchilotheca elegans* hitherto was not known, but is present in numerous specimens from both Dzheroi and Tashkura (Figs 72-79). It is clearly divided, contrary to the type species of *Euchilotheca*, into protoconchs-1 and 2. The initial part is cylindrical to very slightly swollen, with a rounded tip, and a diameter of c. 70-80  $\mu$ m. A conical, gradual connection leads to a swelling representing protoconch-2, reaching a diameter of c. 160-250  $\mu$ m, situated at a distance of c. 300-375  $\mu$ m from the tip. Protoconch-2 is connected to the teleoconch by a weak and gradual constriction, after which the

**Figs 51-59**. *Camptoceratops priscus* (Godwin-Austen, 1882). **51-57**, RGM 570 823a-g, Tashkura UZ 404; **58-59**, RGM 429 745a-b, paratypes of *Camptoceratops americanus* Garvie in Hodgkinson et al., 1992, Ridge Creek (USA, Texas, Bastrop Co.), E of Upton; Reklaw Formation, Marquez Shale Member (Eocene, Ypresian). Bar 200 μm.

shell attains its adult elongately conical shape. Transverse section of the shell is circular all over its height. The larval shell is variable in slenderness, as demonstrated by Figs 72 and 73.

In many specimens in a more adult stage the (former) presence of a septum is clearly indicated (Figs 60-64, 66-69). The very different diameters of these septa indicate that shedding of an earlier part of the shell occurred several times during the animal's lifetime. In Fig. 79 a stage preceding septum formation, in the form of a clear constriction in the internal mould, seems probable.

Material examined. – RGM 570 825/many, RGM 570 826/10 protoconchs, Dzheroi UZ 250B; RGM 570 827/many, RGM 570 828/many juveniles/protoconchs, RGM 570 829a-e/5 (Figs. 60-64), Dzheroi UZ 260; RGM 570 830/many, RGM 570 831/17 protoconchs, RGM 570 832a-c/3 (Figs. 65-67), Dzheroi UZ 262; RGM 570 833/many, RGM 570 834/many protoconchs, RGM 570 835a-c/3 (Figs 77-79), RGM 570 836/7 fragments retaining apertural margin, Tashkura UZ 404; RGM 570 837/many, RGM 570 838/22 protoconchs, RGM 570 839/1 (Fig. 68), Tashkura UZ 405; RGM 570 840/many, RGM 570 841/many protoconchs, RGM 570 842ah/8 specimens retaining protoconch (Figs 69-76), Tashkura UZ 406.

Discussion. – Just as known from the related species *Euchilotheca succincta* (Defrance, 1828) (see Tembrock, 1965, pl. 7, fig. 1) or *Creseis cylindrica* Hodgkinson (in Hodgkinson et al., 1992, pl. 8, fig. 12) also empty shells of the present species tend to fit into each other when concentrated on the sea bottom after death. This observation led Tembrock erroneously to the supposition that some specimens of *E. succincta* have a double annulation. Numerous specimens in the Tashkura material show that this fitting-together happened frequently, and sometimes even by several specimens. What remains is only the most solid part of the shell, a thickened apertural margin, otherwise only preserved on some isolated fragments. Two specimens showing such 'annulations' are illustrated herein as Figs 70 and 71.

(next page) **Figs 60-71**. *Euchilotheca elegans* Harris, 1894. **60-64**, RGM 570 829a-e, Dzheroi UZ 260; **65-67**, RGM 570 832a-c, Dzheroi UZ 262; **68**, RGM 570 839, Tashkura UZ 405; **69-71**, RGM 570 842a-c, Tashkura UZ 406. Bar 500 μm.





Family Praecuvierinidae Janssen, 2006.

*Texacuvierina* Janssen, 2005 Type species (by original designation): *Cuvierina gutta* Hodgkinson, in Hodgkinson et al., 1992 (Eocene).

Texacuvierina gutta? (Hodgkinson, 1992) (Fig. 80)
Cuvierina gutta Hodgkinson, new species; Hodgkinson, in Hodgkinson et al., 1992: 32, pl. 11 figs 7-10.
Texacuvierina gutta (Hodgkinson) – Janssen, 2005: 35.

Description. – A single specimen deviates from the numerous *Euchilotheca* specimens in the Tashkura samples by its shape. Its dimensions are H = 2.88 + mm, W = 1.20 mm. The apical part is truncated by a distinct, slightly convex septum. After a short conical part with somewhat concave sidelines the shell slowly increases in diameter, but towards its apical part the diameter decreases again, resulting in a barrelshaped outline. Apertural parts are missing. The transverse section is circular, both in apical and in apertural views. Shell surface is smooth, in very low angle light some very weak annulations become visible in the basal shell part.

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Material examined. - RGM 570 843/1 (Fig. 80), Tashkura UZ 406.

Discussion. – At first glance this specimen strongly resembles the species *Texacuvierina gutta*. Especially the shape of the basal part of the holotype (pl. 11, fig. 10 in Hodgkinson et al., 1992) agrees very well with the Tashkura shell. However, the completely preserved holotype of *C. gutta* reaches a shell height of 2.2 mm only and is dorso-ventrally flattened towards the aperture, a feature not demonstrable in the present specimen. Also *T. gutta*, described from the Cook Mountain Formation of Texas, USA, has an age of latest Lutetian/earliest Bartonian (nannoplankton zone NP 16), which certainly is much younger than the Tashkura material. Because of these discrepancies I apply the name with a query only.

(previous page) Figs 72-79. Euchilotheca elegans Harris, 1894, specimens retaining protoconch. 72-76, RGM 570 842d-h, Tashkura UZ 406; 77-79, RGM 570 835a-c, Tashkura UZ 404. Bar 100  $\mu$ m.



Fig. **80**. *Texacuvierina gutta*? (Hodgkinson, 1992). RGM 570 843, Tashkura UZ 406. Bar 500 µm.

Superfamily Cymbulioidea Gray, 1840 Family Cymbuliidae Gray, 1840 Subfamily Cymbuliinae Gray, 1840

# Cymbulia Péron & Lesueur, 1810

Type species (by original designation; see Janssen, 2007: 162): 'Cymbulie Proboscidée' = *Cymbulia proboscidea* Lamarck, 1816 (nomen oblitum) = *Cymbulia peroni* de Blainville, 1818 (nomen protectum) (Recent).

Cymbulia spec. (Fig. 81)

Description. – A restricted number of very small, sinistral specimens resemble closely shells described as *Cymbulia* spec. from Holocene/Recent deposits in the Red Sea (Janssen, 2007; Figs 82 and 83 herein). They are characterized by just 1¼ to 1¾ convex whorls that very rapidly increase in diameter, resulting in a very wide, circular aperture. Similar specimens, only slightly smaller in size





and with a relatively still larger aperture, were isolated from the Uzbekistan samples.

Material examined. – RGM 570 844/4, Dzheroi UZ 250B; RGM 570 845/8, RGM 570 846/1 (Fig. 81), Dzheroi UZ 260; RGM 570 847/15, Dzheroi UZ 262.

Discussion. – Adult specimens of Cymbuliidae have no shell, but an internal gelatinous so-called pseudoconch. A shell is only present during the larval stage, and is shed during metamorphosis of the veliger larva. The minute larval shells of holocene-Recent *Cymbulia* cannot yet be related to the few known living species. The similarity of the fossil specimens with the presently known holocene-Recent larval shells is such that I do not doubt their belonging to the same genus. This is a considerably older occurrence of the genus than could currently be suspected.

## BIOSTRATIGRAPHICAL NOTES

Species distribution over the various samples is represented in Fig. 84. The distribution of two species, *Limacina pygmaea*  and *Camptoceratops priscus*, suggest an immediate correlation with the pteropod zones 9 and 10, as described for the North Sea Basin (Janssen & King, 1988). Samples UZ 405 and UZ 404, in which *C. priscus* is commonly present, can be linked to pteropod-zone 9 and the middle part of nannofossil zone NP13. The four other samples, yielding abundant *L. pygmaea* point to pteropod zone 10 and the interval base NP14 up to the lower part of NP15. The latter species, however, generally regarded as being of Lutetian age, was occasionally also recorded from Ypresian sediments (Curry, 1982; Cahuzac & Janssen, 2010; Janssen, 2010). Such occurrences were interpreted as incidental intrusions into a basin during sea level highstands. Its occurrence, however, in larger numbers still is considered an index for pteropod zone 10.

We redefine here the boundary between Pteropod Zones 9 and 10 by the LOD of *C. priscus,* preventing confusion caused by possible, local, earlier occurrences of *L. pygmaea.* As samples UZ 406 and UZ 260, according to the nannofossil interpretation belong to zone NP 14a (Ypresian) the boundary between pteropod zones 9 and 10 does no longer coincide with the Ypresian/Lutetian boundary as a result of the new definition by GSSP in the Gorrondatxe section (NW Spain) (see above).

Another species, *Limacina erasmiana*, also is found only in the two samples yielding *Camptoceratops*. It was recently introduced from the North Sea Basin Ypresian, but will soon be published from the same interval in Kazakhstan (King et al., MS in prep.). So there seem to be little doubt on an Ypresian age for samples UZ 405 and UZ 404. A somewhat longer presence must be accepted for *Altaspiratella multispira*, so far only known from the Ypresian of S France, but in few specimens found to be present in sample UZ 262 from Dzheroi, that according to the nanno-zonation is already NP 15 (early Lutetian). Additionally, *Heliconoides mercinensis*, common in samples UZ 405, UZ 404 and UZ 406 indicates an Ypresian age. The species is, however, absent in UZ 260, which is supposed to be from the same level.

Sample UZ 406 and the three Dzheroi samples are all characterized by the abundance of *Limacina asiatica* and *L. pygmaea*, and the presence of *L. dzheroiensis*. Two of these are introduced in the present paper. *Limacina asiatica* is known in a single specimen from the Ypresian of Gan and presum-

	Tashkura			Dzheroi		
	UZ 405	UZ 404	UZ 406	UZ 260	UZ 262	UZ 250B
	Alay Formation			Turkestan Formation		
Pterotrachea sp.	-	2	-	r	-	rr
Altaspiratella multispira		-	rr	r	r	-
Heliconoides mercinensis	CC	CC	CC	-	-	-
Heliconoides aff. paula	-	r	-	-	-	-
Limacina asiatica	-	-	CC	CC	CC	CC
Limacina dzheroiensis	-	-	r	с	r	rr
Limacina erasmiana	с	cc	-	-	-	-
Limacina pygmaea		-	CC	cc	CC	CC
Limacina cf. smithvillensis		-	-	cc	r	-
Limacina vegrandis	С	CC	С	с	rr	r
Camptoceratops priscus	c	cc	-	-	-	-
Euchilotheca elegans	cc	cc	cc	CC	CC	CC
Texacuvierina gutta ?	-	-	rr	-	-	-
<i>Cymbulia</i> sp.	-	-	-	r	с	r
Pteropod zones	later part of zone 9		early part of zone 10			
Nannoplankton zones	NP 13		NP 14		NP 15	
Chronostratigraphy	Ypresian				Lutetian	

rr = 1; r = 2 -10; c = 11 - 50; cc = > 50 specimens

Fig. **84**. Species distribution over the various samples, with pteropod and nannoplankton zonation.

ably, also in a single specimen, from the Lutetian of Japan. *Limacina dzheroiensis* is, with some doubt, also recorded from the Lutetian of the North Sea Basin (see above).

The common presence of *Euchilotheca elegans* in all samples suggests that we are dealing with the later part of pteropod zone 9 and the early part of zone 10, which agrees well with the identification of nannofossil zones NP 13-NP 15, but the presence of a larger hiatus at the boundary of the Alay and Turkestan formations is not reflected in the pteropod distribution, as obviously some pteropod species straddle the Ypresian/Lutetian-boundary.

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#### References

- ANDO, Y., UJIHARA, A. & ICHIHARA, T., 2009. First occurrence of Paleogene pteropods (Gastropoda; Thecosomata) from Japan. – Journal of the Geological Society of Japan 115: 187-190.
- AUBRY, M.-P. & BORD, D., 2009. Reshuffling the cards in the photic zone at the Eocene: Oligocene boundary. In: Koeberl, C. & Montanari, A. (eds). The Late Eocene Earth. – The Geological Society of America, Special Paper 452: 279-301.
- AVERIANOV, A.O., 1997. Paleogene sea snakes from the eastern part of Tethys. – Russian Journal of Herpetology 4: 128-142.
- BANDEL., K, & HEMLEBEN, C., 1987. Jurassic heteropods and their modern counterparts (planktonic Gastropoda, Mollusca). -- Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 174: 1-22.
- BERGGREN, W.A. & PEARSON, P.N., 2005. A revised tropical Paleogene planktonic foraminiferal zonation. – Journal of Foraminiferal Research 35: 279-298.
- BOUCHET, P., & ROCROI, J.-P., 2005. Classification and nomenclator of gastropod families. – Malacologia 47: 1-397.
- CAHUZAC, B., & JANSSEN, A.W., 2010. Eocene to Miocene holoplanktonic Mollusca (Gastropoda) of the Aquitaine Basin, southwest France. – Scripta Geologica 141: 1-193.
- CASE, G.R., UDOVICHENKO, N.I., NESSOV, L.A., AVERIANOV, A.O. & BORODIN, P.D., 1996. A Middle Eocene selachian fauna from the White Mountain formation of the Kizylkum Desert, Uzbekistan, C.I.S. – Palaeontographica A 242: 99-126.
- CURRY, D., 1965. The English Palaeogene pteropods. Proceedings of the Malacological Society of London 36: 357-371.

CURRY, D., 1982. Ptéropodes éocènes de la tuilerie de Gan (Pyrénées-Atlantiques) et de quelques autres localités du SW de la France. – Cahiers de Micropaléontologie 4 (1981): 35-44.

DALIMOV, T.N. ET AL. (49 authors), 1998. Geology and minerals of the republic of Uzbekistan. Tashkent: 723 pp. (in Russian).

- EAMES, F.E., 1952. A contribution to the study of the Eocene in western Pakistan and western India, C. The description of the Scaphopoda and Gastropoda from standard sections in the Rakhi Nala and Zinda Pir areas of the western Punjab and in the Kohat district. – Philosophical Transactions of the royal Society of London (B)236(631): 1-168.
- GODWIN-AUSTEN, H.H., 1882. On a fossil species of *Camptoceras*, a freshwater mollusk from the Eocene of Sheerness-on-Sea. – Quarterly Journal of the Geological Society of London 38: 218-221.
- HARRIS, G.F., 1894. On the discovery of a pteropod in British Eocene strata, with the description of a new species. – Proceedings of the Malacological Society of London 1: 61-62.
- HERRMANNSEN, A.N., 1846-1849. Idicis generum malacozoorum primordia. Nomina subgenerum, generum, familiarum, tribuum, ordinum, classium; adjectis auctoribus, temporibus, locis systematicis atque literariis, etymis, synonymis. Praetermittuntur Cirripedia, Tunicata et Rhizopoda 1-2: i-xxvii, 1-637, 1846 (1); i-xlii, 1-717, 1847-1849 (2). Cassellis.

- HODGKINSON, K.A., GARVIE, C.L. & Bé, A.W.H., 1992. Eocene euthecosomatous Pteropoda (Gastropoda) of the Gulf and eastern coasts of North America. – Bulletins of American Paleontology 103(341): 5-62.
- JANSSEN, A.W., 2003. Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 13. Considerations on a subdivision of Thecosomata, with the emphasis on genus group classification of Limacinidae. – Cainozoic Research 2: 163-170.
- JANSSEN, A.W., 2005. Development of Cuvierinidae (Mollusca, Euthecosomata, Cavolinioidea) during the Cainozoic: a non-cladistic approach with a re-interpretation of Recent taxa. – Basteria 69: 25-72.
- JANSSEN, A.W., 2006. Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 16. Some additional notes and amendments on Cuvierinidae and on classification of Thecosomata (Mollusca, Euthecosomata. – Basteria 70: 67-70.
- JANSSEN, A.W., 2007. Holoplanktonic Mollusca (Gastropoda) from the Gulf of Aqaba, Red Sea and Gulf of Aden (Late Holocene-Recent) – The Veliger 49: 140-195
- JANSSEN, A.W., 2010. Pteropods (Mollusca, Euthecosomata) from the Early Eocene of Rotterdam (The Netherlands). – Scripta Geologica

Special Issue 7: 161-175.

- JANSSEN, A.W., & KING, C., 1988. Planktonic molluscs (Pteropods). In: Vinken, R. et al. (eds). The northwest European Tertiary Basin. Results of the International Geological Correlation Programme Project no. 124. – Geologisches Jahrbuch (A)100: 356-368.
- JANSSEN , A.W., SCHNETLER, K.I. & HEILMANN-CLAUSEN, C., 2007. Notes on the systematics, morphology and biostratigraphy of fossil holoplanktonic Mollusca, 19. Pteropods (Gastropoda, Euthecosomata) from the Eocene Lillebaelt Clay Formation (Denmark, Jylland). – Basteria 71: 157-168.
- JANSSEN, A.W. & ZORN, I., 1993. Revision of Middle Miocene holoplanktonic gastropods from Poland, published by the late Wilhelm Krach. In: Janssen, A.W. & Janssen, R. (eds). Proceedings of the Symposium Molluscan Palaeontology, 11th International Malacological Congress, Siena, Italy, 30th August-5th September 1992. – Scripta Geologica Special Issue 2: 155-236.
- KROHN, A., 1860. Beiträge zur Entwicklungsgeschichte der Pteropoden und Heteropoden: 1-45. Leipzig.
- LAMARCK, [J.B.P.A. DE], 1805-1806. Mémoire sur les fossiles des environs de Paris, comprenant la détermination des espèces qui appartiennent aux animaux marins sans vertèbres, et dont la plupart sont figurées dans la collection des vélins du Muséum, 5. – Annales du Muséum d'Histoire naturelle de Paris 5: 28-36, 91-98, 179-188, 237-245, 349-357.
- LAMARCK, [J.B.P.A. DE], 1806. Explications des planches relatives aux coquilles fossiles des environs de Paris. Explication des planches XI à XIV. – Annales du Muséum d'Histoire naturelle de Paris 8: 383-388.
- LUTERBACHER, H.-P., ALI, J.R., BRINKHUIS, H., GRADSTEIN, F.M., HOOKER, J.J., MONECHI, S., OGG, J.G., POWELL, J., RÖHL, U., SANFILIPPO, A. & SCHMITZ, B., 2004. The Paleogene Period. In: Gradstein, F.M., Ogg, J.G. & Smith, A. (eds). A Geologic Time Scale 2004: 384-408. Cambridge, UK
- MARTINI, E., 1971, Standard Tertiary and Quaternary calcareous nannoplankton zonation. In: Farinacci, A. & Matteucci, R. (eds). Proceedings of the II Planktonic Conference, Roma, 1970, 2: 739-785. Rome.
- MIRKAMALOVA, S.K., 1958. Stratigraphy and mollusc faunas of the Pretashkent area and Kysyl-Kum: 1-128. Moscow (in Russian).
- Molina, E., Alegret, L., Apellaniz, E., Bernaola, G., Caballero, F., Di-Narès-Turell, J., Hardenbol, J., Heilmann-Clausen, C., Larrasoaña, J.C., Luterbacher, H., Monechi, S., Ortiz, S., Orue-Etxebarria, X., Payros, A., Pujalte, V., Rodríguez-Tovar, F.J., Tori, F., Tosquella, J. & Uchman, A., 2011. The Global Standard Stratotype Section and

Point (GSSP) for the base of the Lutetian Stage at the Gorrondatxe section (Spain). – Episodes, 34(2): 86-108.

- MOROZOV, S.D, RASULOV, W.M., BOYKO, V.S. & TROITSKY, V.I., 1988. Geology of the Paleogene sediments of the south-eastern Kyzyl Kum: 1-139. Tashkent (in Russian).
- NESSOV, L.A., SHABANINA, N.V. & UDOVICHENKO, N.I., 1987. New localities of vertebrate remains in the Middle Eocene phosphorites of Central Kyzylkum and conditions of granular phosphorite formation. – Uzbekskiy Geologicheskiy Zhurnal 4: 72-77 (in Russian).
- NEWTON, R.B., 1891. Systematic list of the Frederic E. Edwards collection of British Oligocene and Eocene Mollusca in the British Museum (Natural History), with references to the type-specimens from similar horizons contained in other collections belonging to the geological department of the Museum: i-xxviii, 1-365. London.
- ORUE-EXTEBARRIA, X., PAYROS, A., BERNAOLA, G., DINARES-TURELL, J., TOSQUELLA, J., APELLANIZ, E. & CABALLERO, F., 2006. The Ypresian/Lutetian boundary at the Gorrondatxe beach section (Basque Country, W Pyrenees). – Mid-conference excursion guidebook of the International Meeting on Climate and Biota of the Early Paleogene University of the Basque Country, Bilbao, Spain.
- PERCH-NIELSEN, K., 1985. Cenozoic calcareous nannofossils. In: Bolli, H.M., Saunders, J.B. & Perch-Nielsen, K. (eds.). Plankton Stratigraphy. – Cambridge Earth Science Series 11: 427-554.
- RAMPAL, J., 1973. Phylogénie des ptéropodes thécosomes d'après la structure de la coquille et la morphologie du manteau. – Comptes Rendues de l'Académie des Sciences de Paris 277(D): 1345-1348.
- RAMPAL, J., 1975. Les thécosomes (mollusques pélagiques). Systématique et évolution - écologie et biogéographie méditerranéennes: 1-485. Aix-Marseille (thesis Univ. Provence CNRS AO 11932) (unpublished).
- RICHTER, G., 1968. Heteropoden und Heteropodenlarven im Oberflächenplankton des Golfes von Neapel. – Pubblicazioni della Stazione Zoologica di Napoli 36: 347-400.
- SEAPY, R.R., 2008. Pterotracheidae Rafinesque, 1814. Http://tolweb.org/Pterotracheidae/28734/2008.08.14 in The Tree of Life Web Project, http://tolweb.org/.
- SMITH, T., WILDE, B. DE & STEURBAUT, E., 2004. Primitive equoid and tapiroid mammals: keys for interpreting the Ypresian-Lutetian transition of Belgium. – Bulletin de l'Institut royal des Sciences naturelles de Belgique, Sciences de la Terre 74 Supplement: 165-175.
- STEURBAUT, E., 1986. Late Middle Eocene to Middle Oligocene calcareous nannoplankton from the Kallo well, some boreholes and exposures in Belgium, and a description of the Ruisbroek Sand Member. –

Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie 23 (2): 49-83.

- STEURBAUT, E., 1990. Calcareous nannoplankton assemblages from the Tertiary in the Knokke borehole. In: Laga, P. & Vandenberghe, N. (eds.). The Knokke well (11E/138) with a description of the Den Haan (22W/276) and Oostduinkerke (35E/142) wells. – Mémoires pour servir à l'Explication des Cartes Géologiques et Minières de la Belgique 29: 47-62.
- STEURBAUT, E., 1991. Ypresian calcareous nannoplankton biostratigraphy and palaeogeography of the Belgian Basin. In: Dupuis, C., Coninck, J. de & Steurbaut, E. (eds). The Ypresian stratotype. – Bulletin van de Belgische Vereniging voor Geologie 97 (1988): 251-285.
- STEURBAUT, E. & NOLF, D., 1989. The stratotype of the Aalter Sands (Eocene of NW Belgium): stratigraphy and calcareous nannoplankton.
  Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie 26: 11-28.

- ТЕМВRОСК, М.L., 1965. Zur Systematik einiger problematischer Caeciden-Gattungen (Gastropoda). – Mitteilungen Zentrales Geologisches Institut Berlin 1: 81-93.
- THIRIOT-QUIÉVREUX, C., 1969. Organogénèse larvaire du genre *Atlanta* (mollusque hétéropode). Vie et Milieu (A)(biol. mar.) 20: 347-396.
- VAROL, O., 1989. Paleocene calcareous nannofossil biostratigraphy. In: Heck, S.E. van (ed.). Nannofossils and their applications: 267-310. Chichester.
- WATELET, A., & LEFÈVRE, T., 1885. Note sur des ptéropodes du genre Spirialis découverts dans le Bassin de Paris. – Annales de la Société malacologique de Belgique 15 (1880): 100-103.
- WRIGLEY, A.G., 1934. A Lutetian fauna at Southampton Docks. Proceedings of the Geologist's Association 45: 1-16.
- ZHELEZKO, V.I. & KOZLOV, V.A., 1999. Elasmobranchii and Palaeogene biostratigraphy of Trans-Urals and Central Asia: 321 pp. Ekaterinburg (in Russian).