Evolutionary ecology of the Pachydontinae (Bivalvia, Corbulidae) in the Pebas lake/wetland system (Miocene, western Amazonia)

F.P. Wesselingh

Frank P. Wesselingh, Department of Geology, Nationaal Natuurhistorisch Museum, Postbus 9517, 2300 RA Leiden, The Netherlands and Department of Biology, University of Turku, SF-20014 Turku, Finland (wesselingh@naturalis.nnm.nl).

Key words – Corbulidae, Pachydontinae, Miocene, Amazonia, evolution, adaptation.

Miocene deposits in western Amazonia and adjacent areas of South America harbour a diverse suite of endemic corbulid bivalves, commonly referred to as Pachydontinae, that show a wide variety of morphologies. Especially in the Miocene Pebas Formation (Peru, Colombia and Brazil), this group diversified spectacularly. Since these corbulids (a cosmopolitan marine and perimarine bivalve family) occur with freshwater taxa and yield isotope signals strongly indicative of freshwater settings, the success of this group in inland basins of Miocene northwestern South America is surprising. In this paper it is argued that a combination of adaptations to fluid bottom substrates, common dysoxia and high predation intensities explains their abundance, their morphological diversity and the paucity of freshwater bivalve groups, such as Sphaeriidae, Corbiculidae and Unionoidea.

Contents

Introduction

The mollusc fauna of the Miocene Pebas Formation of western Amazonia (Peru, Colombia and Brazil) is dominated by (endemic) representatives of the Pachydontinae (Bivalvia, Corbulidae; Wesselingh *et al.*, 2002; Wesselingh, 2006). These species are endemic to Miocene western Amazonia (Nuttall, 1990) and adjacent Llanos/Magdalena Basins to the north, and possibly the Cuenca Basin to the west (Wesselingh & Macsotay, 2006). The Pebasian Pachydontinae harbour a wide array of morphologies, surpassing the range of forms of the remainder of the corbulid family, a cosmopolitan marine and marginal marine family (with a single, South American, freshwater exception, see below). Since these Pebasian corbulids occur with freshwater taxa and yield isotope signals strongly indicative of freshwater settings (Wesselingh *et al.*, 2002, 2006b; Vonhof *et al.*, 1998, 2003; Kaandorp *et al.*, 2006), the success of this group in inland basins of Miocene

northwestern South America begs an explanation. This paper aims at understanding their abundance, taxonomic richness and exuberant morphologies by investigating autecological properties of the Pachydontinae from the Pebas Formation.

The Pebas lake/wetland system was a huge (> 1 million km^2), shallow system of lakes and wetlands, that straddled the equator in western Amazonia between *c.* 9 and 23 million years (Ma) ago (Wesselingh *et al.*, 2006a). The system experienced similar tropical rainforest-like climates as the region does today (Kaandorp *et al.*, 2005). In the Pebas system, profuse radiations of endemic ostracods (Whatley *et al.*, 1998; Muñoz-Torres *et al.*, 1998, 2006), gastropods and bivalves occurred (Nuttall, 1990; Wesselingh *et al.*, 2002; Wesselingh, 2006). In species numbers the cochliopid snails dominate the Pebas fauna, but in abundance the corbulid bivalves dominate (*c.* 67%: Wesselingh *et al.*, 2002). The bivalve fauna of the Pebas Formation is mainly composed of endemic corbulids, known as the Pachydontinae. One corbulid species, *Corbula cotuhensis* Wesselingh & Anderson *in* Wesselingh, 2006, is found rarely in the Pebas fauna and associated with marine incursion intervals. This species is not part of the endemic Pebasian Pachydontinae. Unionoids (pearly freshwater mussels) occur in low numbers with few species (often dominating marginal lacustrine to fluvial settings). Only three species (*Diplodon indianae* Wesselingh, 2006, *D. longulus* (Conrad, 1874) and *Anodontites batesi* (Woodward, 1871)) have been found *in situ* in lacustrine associations. Two species of dreissenid bivalves lived in the system, where they form the third bivalve group in abundance (typically making up 1% or so of mollusc samples). Corbiculid and sphaeriid clams are very rare in the Pebas fauna, represented by only one and two species respectively, that are non-endemic fluvial species (Wesselingh, 2006). The latter four groups are common constituents of Miocene fluvial faunas in the adjacent Andean regions and of slightly younger faunas from the Amazon region (Nuttall, 1990; Wesselingh *et al.*, 2006c).

The pachydontine corbulids are represented by six genera and 24 species (Nuttall, 1990; Wesselingh, 2006), 16 of which belong to *Pachydon*. Recently, three of the six genera (*Pachydon*, *Ostomya* and *Anticorbula*) have been found in Paleocene deposits of the United States (Anderson *et al.*, 2006), but it appears that the Pebasian *Pachydon* species form one or two endemic clades within the Pebas system. Corbulids are a common constituent of marginal marine and marine soft bottom communities worldwide. They are typically represented by few co-occurring species, with unspectacular, small shells. Various species are opportunists and are capable of dealing with unfavorable conditions such as dysoxic settings. In contrast, the Pebasian corbulids form a remarkable morphological diverse assemblage (Figs. 1-7, 9, 10). The dominance and variety of pachydontine bivalves has been attributed to isolated brackish (anomalohaline) conditions (Nuttall, 1990), which appeared to be corroborated by ostracod data (Whatley *et al.*, 1998). A general brackish nature of the Pebas system was supported by other data that also implied marine connections of the system (among them mangrove pollen, Hoorn, 1993; estuarine fish, Monsch, 1998; tidal sedimentary structures, Räsänen *et al.*, 1998; and brackish ichnofossil assemblages, Gingras *et al.*, 2002). An open (marginal marine) system, however, does not comply with very high rates of endemism in ostracods and molluscs (typically over 90% in abundance; Muñoz-Torres *et al.*, 1998, 2006; Wesselingh *et al.*, 2002; Wesselingh, 2006). Furthermore, a brackish nature conflicts with the presence of pearly freshwater mussels in living position, and the absence of typical marginal marine taxa such as arc shells, oysters, mussels and mangrove cerithoidean snails. Also,
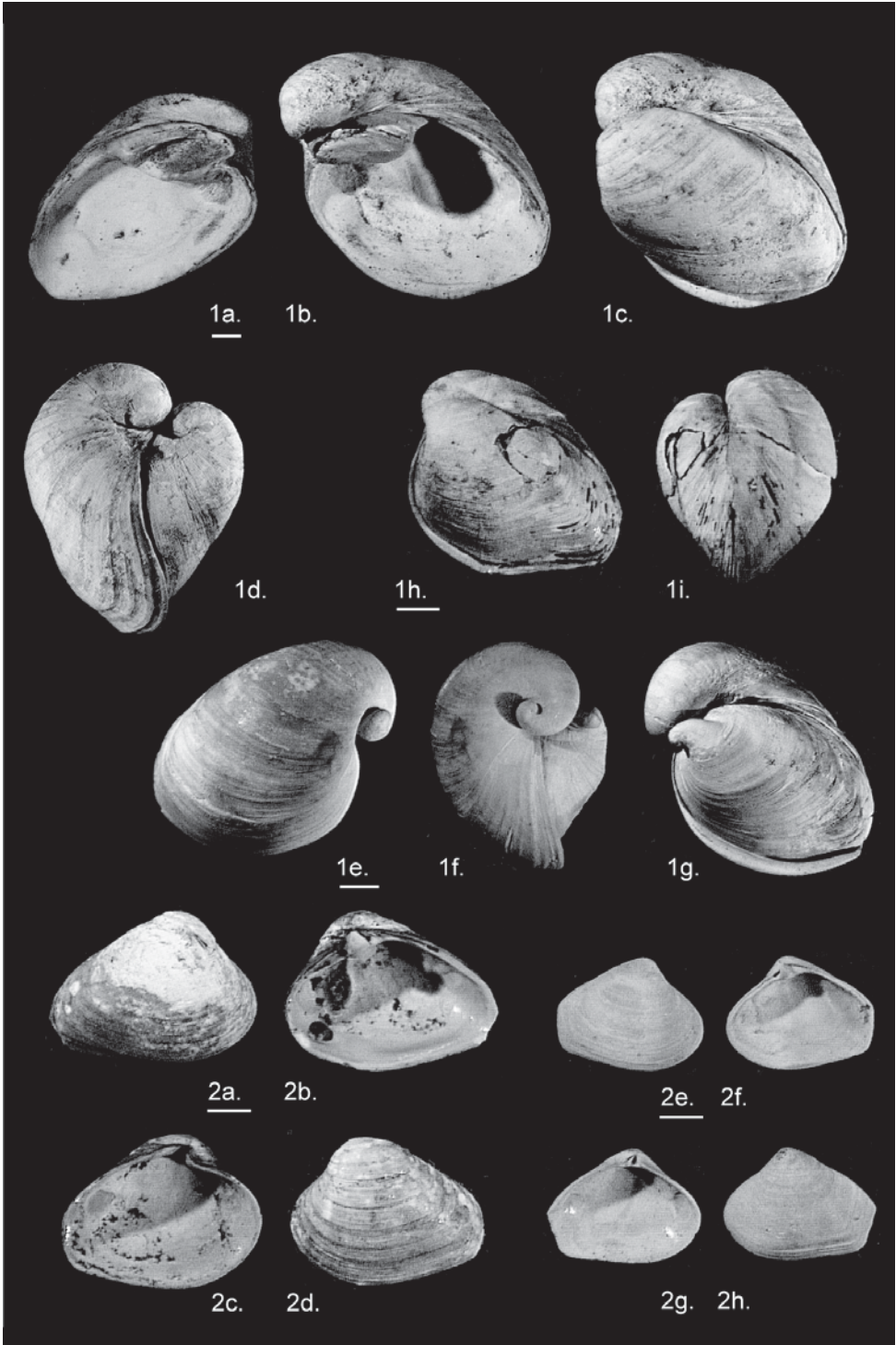
strontium and stable oxygen isotope data point to predominant freshwater settings in the Pebas system (Vonhof *et al.*, 1998, 2003; Wesselingh *et al.*, 2002, 2006b; Kaandorp *et al.*, 2006). If the system was truly freshwater, why are unionoids and corbiculids so scarce? On the other hand, if the system was brackish, why then are cosmopolitan marginal marine groups as arc shells, oysters, mussels and mangrove cerithoideans lacking altogether? They were, after all, present in South American coastal regions at the time. In order to understand the dominance of the pachydontine bivalves in the Pebas system, their living modes need to be understood. Below, nine of the twenty four species present in the middle and upper part of the Pebas Formation (*Crassoretitriletes* and *Grimsdalea* zones of Hoorn, 1993; Middle to early Late Miocene) are shortly diagnosed, followed by an interpretation of morphology in terms of adaptation to specific ecological conditions. Nuttall (1990), Anderson *et al.* (2006) and Wesselingh (2006) provided the systematic background for this discussion.

Pachydontinae occur outside the Pebas system. The oldest records include species of *Pachydon*, *Ostomya* and possibly *Anticorbula* from the Late Cretaceous and Early Paleogene of North America (Anderson *et al.*, 2006). Hitherto, no records older then Early Miocene have been published for South America. During the Early Miocene two *Pachydon* species (*P. hettneri* and *P. cebada*) lived in the Subandean foreland basins from Venezuela (Wesselingh & Macsotay, 2006; Wesselingh, 2006) south to central Peru. Also, *Anticorbula miocaenica* had a wider distribution to include western Amazonia and northern Venezuela. Contemporary Pebasian records of *Pachydon* possibly include doubtfully identified material from the Cuenca Basin (Ecuador) and the Llanos Basin (Colombia and Venezuela; Nuttall, 1990; Wesselingh *et al.*, 2006a). Records of Pachydontinae post-dating the Pebas Formation are restricted to *Anticorbula*; *A. mencheri* (Pliocene, Venezuela and possibly Trinidad) and *A. fluviatilis* (Recent, Guyana rivers and estuaries, Amazon and adjacent rivers from Santarem, Brazil, possibly up to Iquitos, Peru) (Nuttall, 1990; Leistikow & Janssen, 1997; Anderson *et al.*, 2006). *Anticorbula fluviatilis*, the single extant pachydontine, is a freshwater epibyssate (and possibly partially endobyssate) nestler.

Description and ecological inference of nine Pebasian pachydontine species

Nine species that are characteristic for the Pebas Formation are diagnosed and their morphologies are interpreted in terms of ecology. In the section thereafter, the other pachydontine species are briefly discussed.

Pachydon obliquus Gabb, 1869 – This species has some unusual shell characteristics for a corbulid (Fig. 1). It is a globose small-medium sized *Pachydon* (L 8-17 mm) that has strongly inaequivalve and inaequilateral shells, with highly incurved umbones (Fig. 1e-g). The hinge is extremely robust. The pallial line is located far from the shell's margin, although a deep cavity exists behind the hinge plate, apparently to compensate for the loss of living space near the shell edge (Nuttall, 1990). The shell is markedly thickened near the umbones and at the anterior margin. Especially, the anterior adductor scar is deeply embedded and very prominent. The shell's rim outside the pallial line is much thicker than inside, which appears to be corroded. A pallial sinus is very shallow or lacking. Together with the massive and complex hinge, a furrow in the right valve
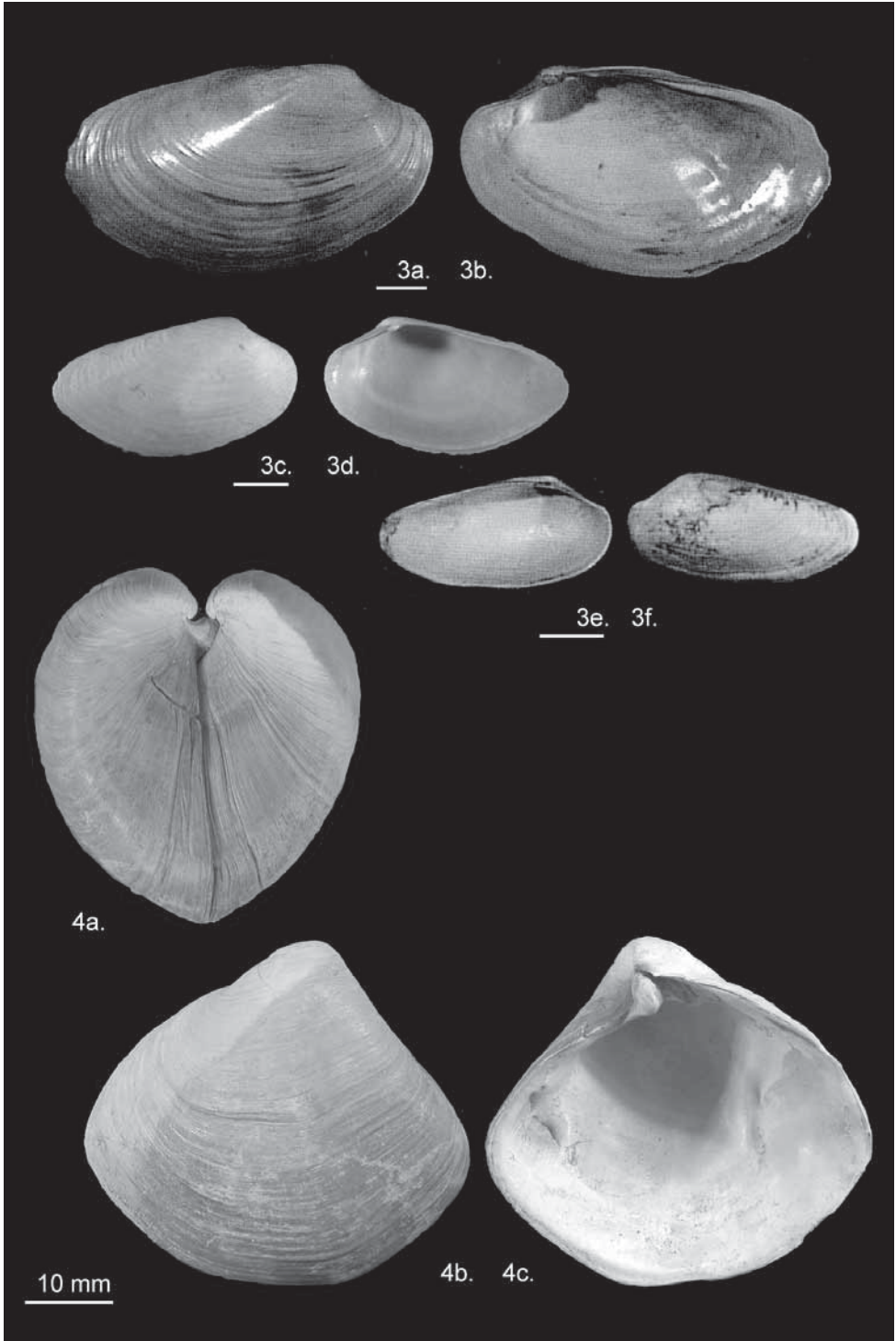
(RV) in which the left valve (LV) fits, forms a system that tightly interlocks the valves. Estimates from growth lines (that are often poorly and irregularly developed) suggest ages between four and ten years for adult specimens. *Pachydon obliquus* is the most common species of the Pebas fauna. Apart from fluviolacustrine settings, it was present in all lacustrine biotopes (Wesselingh *et al.*, 2002). The species is dominant in organic-rich clay intervals that presumably represent dysoxic fluid mud depositional settings. It is curious to develop thick shells to live in such unconsolidated substrates. The shell's point of maximum density provides a clue; it is clearly located near the posterior margin, towards the umbo. This suggests that the umbones anchored the shell into the substrate. Both the thickness of the shell, valve overlap, deep attachment of the mantle margins onto the shell and its general globose nature are features that might have deterred predation (Fig. 1h, i). The vacation of the interior shell margins was compensated by a deep umbonal cavity creating a well-protected living place for the animal.

Pachydon trigonalis Nuttall, 1990 – A small species (Fig. 2) whose shell length typically ranges between 6 and 10 mm. This triangular species has a solid shell with a truncate posterior margin. A robust, but rounded posterior ridge lent extra strength to the shell. The pallial sinus is short, indicating this species to be a shallow burrower. The pallial line is located very far from ventral commissure. *Pachydon trigonalis* abruptly replaced *P. obliquus* as the dominant species in the upper part of the Pebas Formation. The turnover coincided with an interval of marine influence (Wesselingh & Salo, 2006). *Pachydon trigonalis* occupied most parts of the ecosystem, ranging from fluvial influenced marginal lacustrine settings to fluid mud bottoms of the lake proper. In lacustrine clayish intervals specimens tend to be small and thin-shelled (W adult *c.* 6-7 mm), in more coarse-grained marginal lacustrine settings with fluvial influences shells are larger (W *c.* 10 mm), thicker and more inflated (compare Fig. 2a-d and 2e-h). Suggested ages from growth line counts average 5.5 (SD 1.4; n = 31) and 5.6 (SD 1.4; n = 20) years in a 'lacustrine' and a 'fluviolacustrine' population respectively. This indicates the smaller size in the former to be the result of slower growth, not of shorter life spans.

◀   All specimens from the Miocene Pebas Formation unless stated otherwise. Scale bars represent 2 mm in these and other figures unless stated otherwise.

Fig. 1. *Pachydon obliquus*. a-d, RGM 456 192, Santa Rosa de Pichana, Loreto, Peru. a, LV interior. b, RV interior. c, Pair, view from LV. d, Anterior view of pair. e-g, RGM 456 193, Puerto Almendras, Loreto, Peru. This specimen is strongly coiled (1.5 revolution). e, RV exterior. f, Anterior view pair. g, LV view of pair. h, i, RGM 456 194, Iquitos, Puerto Ganso-Azul, Loreto, Peru. The specimen survived a cracking-type predator attack and continued growth after. If the specimen were flatter, the cracking effort probably would have succeeded. h, LV view of pair. i, Posterior view of pair.

Fig. 2. *Pachydon trigonalis*. a-d, RGM 456 195, Puerto Nariño, Amazonas, Colombia. Specimen from marginal (riverine influenced) lacustrine assemblage. a, RV exterior. b, RV interior. c, LV interior. d, LV exterior. e-h, RGM 456 196, Los Chorros, Amazonas, Colombia. Specimen from lacustrine assemblage, notably smaller and thinner then specimens from marginal lacustrine settings. e, RV exterior. f, RV interior. g, LV interior. h, LV exterior.
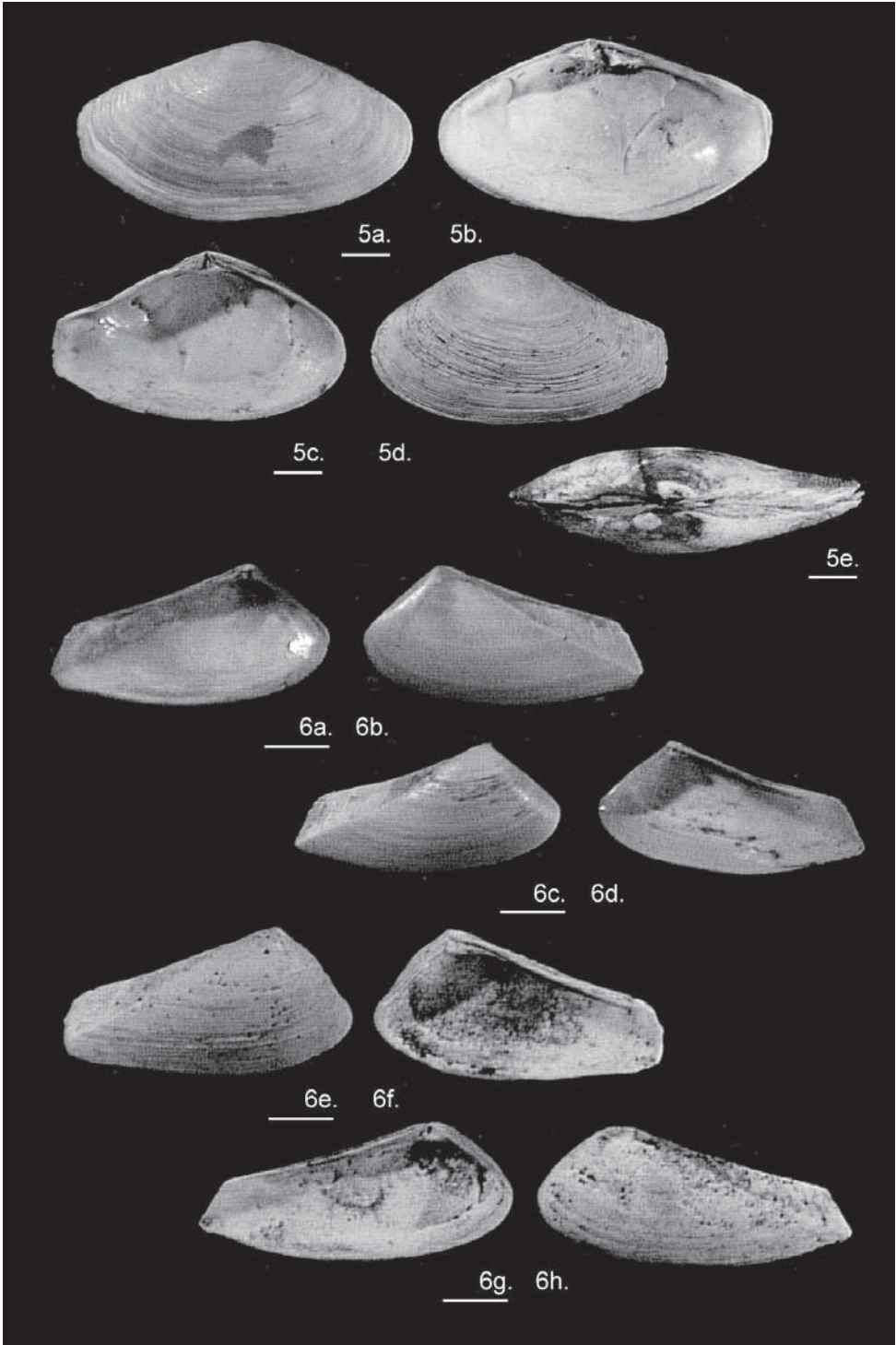
Pachydon amazonensis (Gabb, 1869) – This is a medium-sized (W 7-20 mm), elongate, oval-shaped *Pachydon* species (Fig. 3). It is aequivalve and comparatively thin-shelled. From counts of growth lines ages of 4-9 years are estimated. Variations in shell outlines and sizes exist. Smaller shells can be either elongate ovate (Fig. 3c, d) or elongate tapering, with a slightly truncate posterior margin (Fig. 3e, f). The apex is located between one fifth and one eight from the anterior margin. Smaller ovate-shelled populations tend to have rather convex shells (in cross section); specimens from populations with very large shells are comparatively flatter. The cardinal tooth is small in comparison with other *Pachydon* species. The lateral grooves are well developed. The adductor scars and the pallial line are very shallow. The pallial sinus is truncate, suggesting shallow burrowing behaviour. A furrow may develop in the RV just inside the ventral margin, marking the location of the LV margin. The shell is thin and often markedly polished. On the interior surface outside the pallial line vague, broad radial striae occur, best developed on the posterior margins. In many specimens the largest height is attained in the posterior half, thereby counteracting the umbonal regions as the centre of gravity. From the shell itself no information about living position can be interpreted, other then a shallow burrowing behaviour on account of the straight, truncate pallial sinus. Given the abundance of shell predators in the Pebas system (see below), the thin shell is a remarkable feature, especially when taking into account that this species only rarely shows signs of (failed) predation. One scenario could be that almost every attack resulted in the destruction of the whole shell. Another possibility is shown by the Chinese unionoid *Soleinaia oleivora* (Savazzi & Peiyi, 1992) that combines inefficient burrowing and a distasteful sulphur-laden animal with a shell that forms a rather poor defence against predation (alike thin-shelled specimens of *P. amazonensis)*. The radial striae on the interior of *P. amazonensis* may imply a highly retractable mantle, which probably is another defensive adaptation against predators.

Pachydon erectus Conrad, 1871 – This, the largest of the Pebasian corbulids, attains sizes of L 55 mm, H 50 mm (Fig. 4). This species has a solid, but thin, shell for its size. It is a tumid, aequivalve, almost triangular species, with a stout anterior ridge that bounds a wide flat to concave anterior platform on which the species can balance. The posterior margin has a slit-like gape with reinforced margins. The shells are somewhat thicker on the anterior side, where the adductor scars and pallial line are more deeply embedded than on the posterior side. The pallial sinus is variable; it may be lacking altogether, but can also be developed as a very irregular indentation, suggesting shallow burial. Oxygen isotope profiles along growth increments (Kaandorp *et al.,* 2006) indicated a 5-year age for an intermediate specimen (W *c.* 30 mm). The largest specimen (W 55 mm) numbered some 14 rings that can be interpreted as years; smaller species (W 25-30 mm) have

Fig. 3. *Pachydon amazonensis*. a-b, RGM 456 197, Santa Elena, Loreto, Peru. a, RV exterior. b, RV interior. c-d, RGM 456 597, Pebas/ Pijoyal (Loreto, Peru). c, RV exterior. d, RV interior. e-f, RGM 456 198, Santo Tomas Amazonas, Loreto, Peru. e, LV interior. f, LV exterior.

Fig. 4. *Pachydon erectus*. RGM 456 199, Santa Rosa de Pichana, Loreto, Peru. a, Anterior view of pair showing the concave, wide posterior platform that presumably enhanced stability in semi fluid substrates. b, RV exterior. c, RV interior.
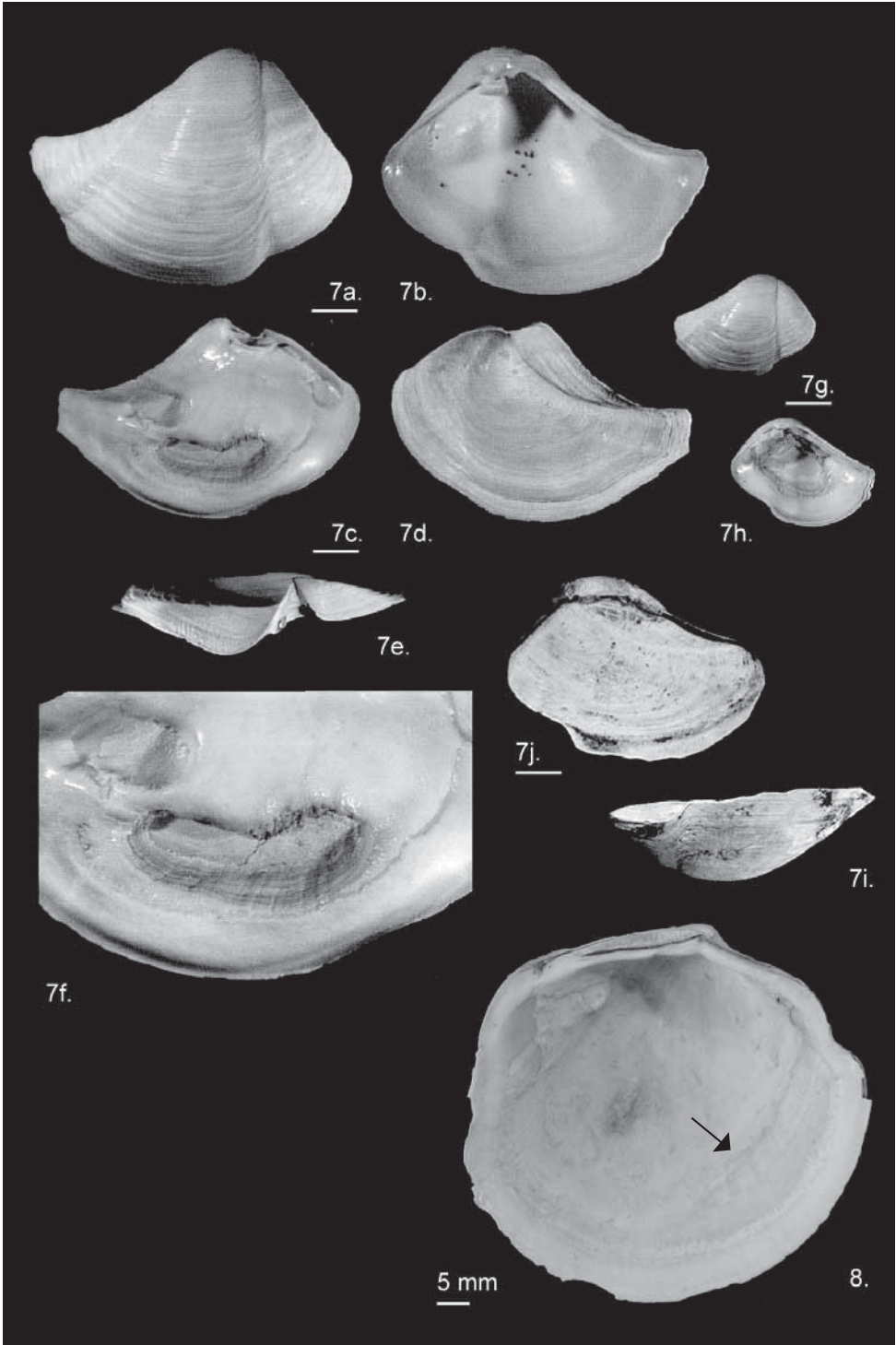
5-7 possibly annual rings, which is in line with the observed isotope age estimates. Many specimens did not yield growth lines regularly enough to be interpreted as year rings. Shell density points to anterior side down orientation. The broad, concave anterior margin may have enhanced an epifaunal or semi-infaunal living mode on soft sediments, ensuring that the shell did not sink deeply into the mud and thus leaving the posterior margins with the siphons close enough to or at the sediment surface to function (iceberg strategy; Thayer, 1975). Kaandorp *et al.* (2006) interpreted, based on relatively subdued seasonal oxygen isotope variation, a lacustrine biotope for this species.

Pachydon telliniformis Wesselingh, 2006 – This species strikingly resembles in outline a number of *Tellina* species (Fig. 5), as indicated by its name. This intermediate-sized (W 10-16 mm), flat and rather thick-shelled species is somewhat inaequivalve. The RV is slightly more convex and larger than the LV, but almost no valve overlap exists apart from the ventralmost point. The shell has a posterior margin that is slightly rostrate. The postero-ventral margins of the LV is slightly concave, giving the valve a more rostrate outline than the RV. The posterior dorsal margin is quite robust. The commissural plane is wavy; the posterior margin is tending to be rostrate and bent (Fig. 5e). From the posterior adductor scar, the pallial line runs without a sinus towards the central part of the ventral margin, leaving a substantial area posteriorly outside the mantle edge attachment. The posterior commissural plane is bent towards the RV, very similar as in various tellinid species, to which is bears a striking resemblance in general outline. Such tellinids from the western Atlantic are deposit feeders that have been shown to burrow until they lay more or less in a plane parallel to and below the sediment surface (Stanley, 1970). Although it is likely that *P. telliniformis* was a (sub)horizontal burrower, nothing is known about its feeding ecology. A subhorizontal living mode would have greatly enlarged its carrying capacity in unstable sediments (snowshoe effect; Thayer, 1975). Specimens from marginal lacustrine sandy depositional environments tend to be somewhat larger, thicker and slightly more inflated then those from lacustrine muddy environments. The species pertained estimated ages between six and seven years, estimated from growth line counts.

Pachydon ledaeformis (Dall, 1872) – An aequivalve species that has very inaequilateral, elongate rostrate shells, resembling elongate crassatelloid shells (Fig. 6). This species is small-intermediate in size (L 8-10 mm) and flat. The apex is located not far from the robust and rounded anterior margin. The posterior end of the shell is tapering. A well-defined ridge that runs from the umbo to the postero-ventral boundary delimits a rostrum-like posterior slope. Shells from muddy lacustrine bottom environments (Fig. 6a-d) tend to be thinner then those from sandy near-shore environments (Fig. 6e-h), but

◀ Fig. 5. *Pachydon telliniformis*. a-b, RGM 456 200, Nuevo Horizonte, Loreto, Peru. a, RV exterior. b, RV interior. c-d, INGEMMET TN32. c, LV interior. d, LV exterior. e, RGM n.n. Dorsal view of pair; note the bent posterior tip.

Fig. 6. *Pachydon ledaeformis*. a-d, RGM 456 201, Santa Elena, Loreto, Peru. a, LV interior. b, LV exterior. c, RV exterior. d, RV interior. e-h, RGM 456 202, Puerto Caiman/Caqueta, Amazonas, Colombia. e, RV exterior. f, RV interior. g, LV interior. h, LV exterior.
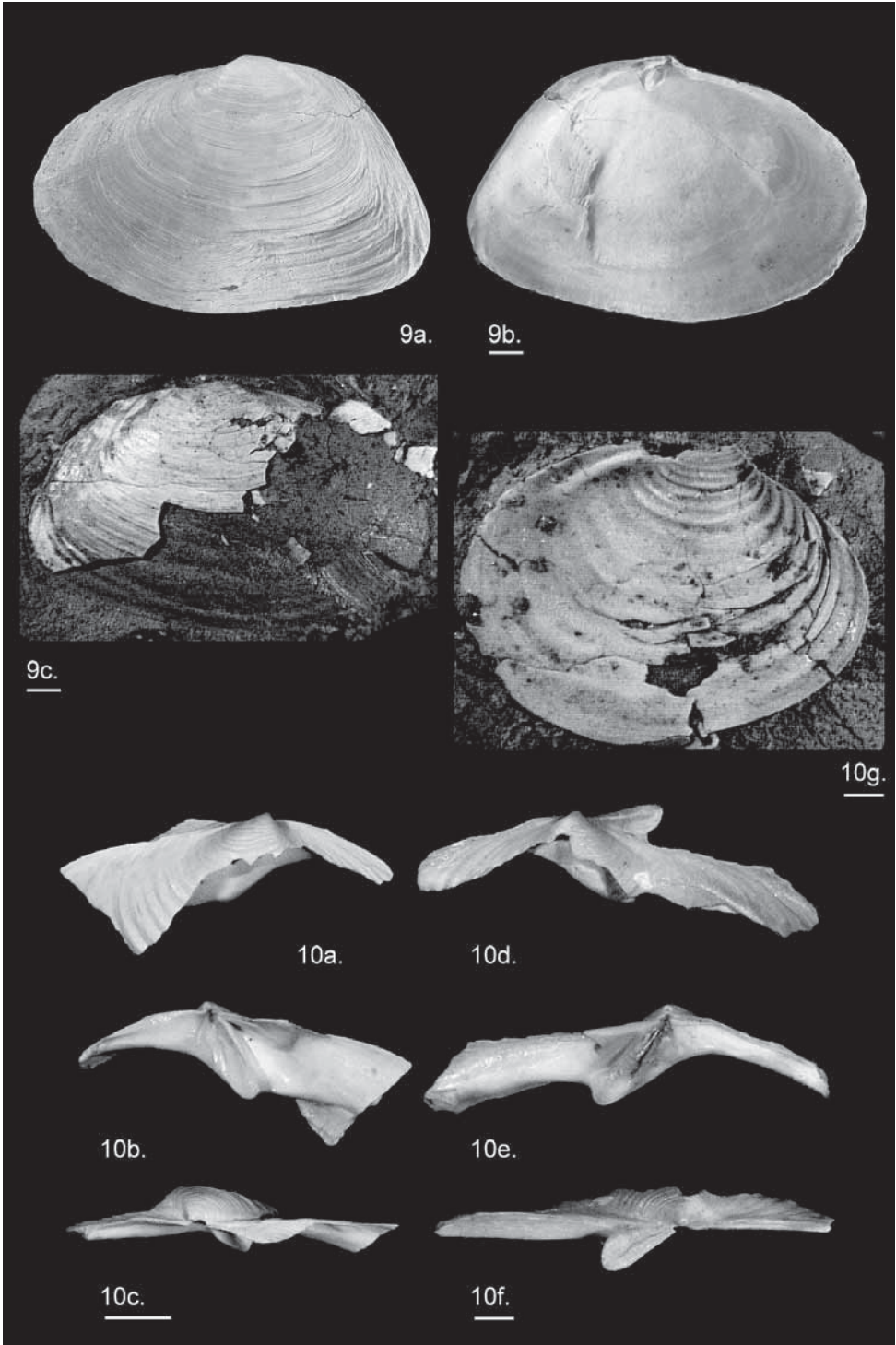
no obvious differences in size were seen. Dentition is not very strong. The pallial sinus is truncate. Growth line counts suggest ages between four and six years. There is no indication of the living position based on the shell, other then that the rostrum might have served as a protection for siphons, possibly indicating a beak-down position. The truncate pallial sinus suggests a shallow burial depth.

Exallocorbula dispar (Conrad, 1874) – This is an intermediate-sized pachydontine (W 14-25 mm) with a remarkable outline (Fig. 7). It has a strongly convex bilobed RV and a concave-flat LV. The dorsal margins are at *c.* 90° position from the commissure (Fig. 7e). The shell has a rounded anterior and a rostrate posterior. The hinge area on the dorsal margin of the LV is also located at an angle of *c.* 90°. The RV has a strong and well-defined overlap with the LV at the posterior two-thirds of the ventral margin (Fig. 7i, j). Typical adult shells reached ages between five and six years, based on growth line counts. The shells are usually not extremely thick, but in some populations extremely thickened shells occur next to normal shells. These hypertrophied shells occur in random size classes, so apparently they are not a geriatric feature. These shells may provide an important clue about the living mode of *Exallocorbula* and other pachydontines. The LV of shells illustrated in Figure 7c-f show a three-fold scarring typical for many of these hypertrophied specimens. The posterior adductor is more deeply embedded then the anterior adductor and both yield a typical brain-like surface structure. It is, however, a circular to elongate-kidney shaped third scar that is located at the centre of the shell just above the pallial line that is most striking. This third scar can be very large (almost one third of the shell L) and bears very well developed radial striae. Its position varies somewhat in different shells. The scar bears a striking resemblance to those seen in marine chemosymbiontic lucinid bivalves (Taylor & Glover, 2000). In this latter group the anterior adductor is greatly enlarged (located in the same area as the third scar of *Exallocorbula*), detached from the mantle line and very similarly striated (Fig. 8). The anterior adductor muscle facilitates chemosymbiosis in the lucinid bivalves in a variety of ways (Taylor & Glover, 2000). In several of the lucinids, a linear impression from the scar towards the apex occurs in the shells interior, which is an impression of an enlarged pallial blood vessel that transports large quantities of blood between the heart and the bacteria-laden gills. Vague, but similar imprints were seen in a few of the studied *Exallocorbula* specimens. This is no certain proof of a chemosymbiontic lifestyle, but the combination of features, including the capability of *Exallocorbula* to live in dysoxic mud, makes it a feasible explanation. The recurring central location of the third scar makes an origin as a repair mark from predatory attack or infestation unlikely. *Exallocorbula* occurs in most shallow lacustrine to offshore lacustrine facies in the Pebas Formation, though it is more common in the latter. In sandy substrates it is larger and thicker

◀ Fig. 7. *Exallocorbula dispar*. a-h, RGM 456 203, Nuevo Horizonte, Loreto, Peru. a, RV exterior. b, RV interior. c, LV interior. Note a third filamentous scar in the interior (also in 7f and 7h). d, LV exterior. e, LV dorsal view. f, Enlargement of scar shown in Fig. 7c. g, RV small specimen, exterior. h, RV interior. i-j, RGM 456 204, Santa Sofia, Amazonas, Colombia (paired specimen). i, Ventral view. j, View from LV.

Fig. 8. *Lucina menardi*. RGM 456 205, Le Bois Gouët, Loire-Atlantique, France, Eocene (Lutetian), Falun de Bois Gouët. LV interior. Note enlarged and striate posterior adductor scar (arrow).

9a.   9b.

9c.

10g.

10a.   10d.

10b.   10e.

10c.   10f.

than specimens from muddy substrates. The concave-convex architecture of the shells resembles a ship form, also seen in, for example, Jurassic gryphaeid bivalves (Savazzi, 1999). In the latter, the form is an adaptation to floating in unstable mud.

Ostomya myiformis Wesselingh, 2006 – Unusual among Pebasian pachydontines, *O. myiformis* has a very large anterior margin (Fig. 9). This intermediate-sized (W 23 mm), flat shell has a slightly trapezoid outline, with a broadly rounded anterior margin and a prominently truncate posterior margin. The postero-dorsal margin is slightly elevated compared to the anterodorsal margin. On the exterior, the shells are riddled with rather irregular concentric growth lines overlain by irregular oblique ridges that indicate the presence of a very thick former periostracum. This is a rare species that is typically found in lacustrine bottom assemblages. No age could be estimated from the material available. Its pallial line is broad and truncate posteriorly. Despite being flat, the shell is robust and is thickened in the posterior region, as shown by the more deeply embedded adductor scars. The posterior adductor scar has strongly calcified striae. No paired specimens have been found, but the loose valves indicate a somewhat undulating commissure, as well as the presence of a very distinct anterior gape. In the LV a very low ridge and furrow are developed near the ventral margin, presumably to fit the RV. The living position of this shell is uncertain. The combination of aequivalve shells with the point of maximum density in the posterior half suggests a (semi-)vertical living position. The flatness of the shell would make it cut like a knife, deep into the substrate.

Concentricavalva concentrica Wesselingh, 2006 – This species combines a massive flat hinge platform with a paper-thin concentrically ribbed shell, superficially resembling Mesozoic '*Posidonia*' (*Bositra*) species (Fig. 10). This medium-sized pachydontine species (W *c.* 21 mm) has several unusual characteristics for a pachydontine shell; the shell is extremely thin, the hinge plate is very broad, the cardinals are completely reduced and broad lateral grooves exist. A prominent lanceolate resilifer that is embedded within the hinge platform dominates the hinges of LV and RV alike. Above the resilifer a deep (RV) or shallow (LV) depression is present that bounds a wing-like erect nymph above. The nymph is particularly prominent in the LV; it is thin and wrinkled in the RV. Apart from more or less regular concentric folds, the shell's exterior is in places corrugated and bears irregular/oblique wrinkles, especially prominent on the margins, that indicate a formerly thick periostracum. Paired specimens seen *in situ* contained almost completely sealed margins, although it cannot be ruled out that post-depositional compaction is responsible for this in part. The shell has a sub-quadrate outline, with the pointed, triangular umbo located at *c.* one third the distance from the anterior margin. No age estimate could be made on the basis of the available material, and the living

Fig. 9. *Ostomya myiformis*. a-b, RGM 456 206, Beiruth, Loreto, Peru. a, RV exterior. b, RV interior. c, RGM 456 207, Los Chorros, Amazonas, Colombia. LV exterior (damaged specimen in matrix).

Fig. 10. *Concentricavalva concentrica*. a-c, RGM 456 208, fragment RV, Nuevo Horizonte, Loreto, Peru. a, Exterior view. b, Interior view. c, Dorsal view. d-f, RGM 456 209, fragment LV, same locality. d, Exterior view. e, Interior view. f, Dorsal view. g, RGM 456 210, damaged interior of LV, Los Chorros, Amazonas, Colombia.

position and characteristics of this species are uncertain. Its overall resemblance with Jurassic 'Posidonia' (Bositra), which was a benthic inhabitant of low-energetic oxygen-stressed sea bottoms (Oschmann, 1994), may provide some comparison for the possible living conditions of C. concentrica. The very thin shell would not have been a match to any predator. The very flat nature of the ventral half of this shell (when paired) may have proved efficient in surviving possible breakage, but more likely C. concentrica lived in oxygen-stressed, fluid muddy environments that were hostile to potential predators. The very flat nature of this species may also have enhanced oxygen absorption (Oschmann, 1994). The comparatively robust hinge-plate of C. concentrica is unlike that of 'Posidonia' (Bositra) and may have counteracted a floating living position.

Table 1. Pachydontinae from the Pebas Formation (systematic treatment in Wesselingh, 2006). The uncertain phylogenetic status of this subfamily within the Corbulidae is discussed by Anderson et al. (2006).

Family Corbulidae Lamarck, 1818
    Subfamily Pachydontinae Vokes, 1945
        Genus *Pachydon* Gabb, 1869
            Pachydon obliquus Gabb, 1869
            Pachydon carinatus Conrad, 1871
            Pachydon tenuis Gabb, 1869
            Pachydon amazonensis (Gabb, 1869)
            Pachydon ellipticus Wesselingh, 2006
            Pachydon andersonae Wesselingh, 2006
            Pachydon cuneatus Conrad, 1871
            Pachydon trigonalis Nuttall, 1990
            Pachydon maaikeae Wesselingh, 2006
            Pachydon hettneri (Anderson, 1928)
            Pachydon cebada (Anderson, 1928)
            Pachydon erectus Conrad, 1871
            Pachydon iquitensis de Greve, 1938
            Pachydon ledaeformis Dall, 1872
            Pachydon telliniformis Wesselingh, 2006
        Genus *Exallocorbula* Nemésio, Aronowsky & Anderson, 2006
            Exallocorbula dispar (Conrad, 1874)
        Genus *Ostomya* Conrad, 1874
            Ostomya papyria Conrad, 1874
            Ostomya myiformis Wesselingh, 2006
            Ostomya carinata Wesselingh, 2006
        Genus *Anticorbula* Dall, 1898
            Anticorbula mencheri (Palmer, 1945)
            Anticorbula miocaenica Wesselingh, 2006
        Genus *Pachyrotunda* Wesselingh, 2006
            Pachyrotunda rotundata Wesselingh, 2006
        Genus *Concentricavalva* Wesselingh, 2006
            Concentricavalva concentrica Wesselingh, 2006

Remarks on other Pachydontinae from the Pebas Formation

The other pachydontine species known from the Pebas Formation (Wesselingh, 2006) are shortly discussed. Table 1 lists all the discussed Miocene South American pachydontine species.

Pachydon carinatus Conrad, 1871, is a very robust, medium-sized, rather straight-sided species, which owes its name to the prominent keel. The RV is convex and much larger then the LV. The LV is low, but very thick. The anterior margin of the shell is particularly thickened. This species is commonest in near-shore assemblages, but does occur in low densities in offshore lacustrine assemblages. The offshore specimens are thinner shelled.

Pachydon tenuis Gabb, 1869, is an intermediate-large, elongate ovate species that is smooth and robust. This species is usually inaequivalve, but aequivalve populations do exist. In inaequivalve pairs, the posterior part of the commissural plane is bent towards the LV, similar to *P. telliniformis* (where it is bent towards the RV instead). Remains of periostracum are often encountered on specimens of *P. tenuis* that lived in near-shore to offshore settings. Oxygen isotope profiles in two specimens show a very subdued seasonal signal typical of a larger (lacustrine) aquatic biotope (Kaandorp *et al.,* 2006).

Pachydon cuneatus Conrad, 1871, is an intermediate-sized, aequivalve species with a wedge-formed shell. The species closely resembles the unrelated extant mactraid *Rangia cuneata* in outline. The latter species lives in shallow (<6 m depth) subtidal, marginal marine environments (e.g., estuaries and lagoons) around the Caribbean (La Salle & de la Cruz, 1985). The wedge-formed shell is believed to enhance digging into the substrate. *Rangia* is euryhaline, with optimal salinities typically between 2 and 15 per mil, but has been recorded in freshwater and in salinities up to 28 per mil (La Salle & de la Cruz, 1985). A combination of low salinity, high turbidity, and a substrate of sand, mud and vegetation is preferred by this species that furthermore can withstand episodic anoxic conditions. Apart for the salinity tolerances, the ecological conditions in which this species occurs strongly resembles general conditions in the Pebas system that harboured the Pachydontinae discussed in this paper.

Pachydon ellipticus Wesselingh, 2006, is a regularly ovate, aequivalved species. The species is found in near-shore to offshore lacustrine assemblages. Its ecology is ill understood, but possibly compares to that of the similarly shelled *P. amazonensis*.

Pachydon andersonae Wesselingh, 2006, is a markedly thick-shelled, robust, elongate species. The very thick shell should have been beneficial in withstanding predatory attacks.

Pachydon maaikeae Wesselingh, 2006, is a small, thick-shelled and rather inflated species. It has a poorly delimited rostrum and, judging from the poorly developed pallial sinus, it was a cumbersome shallow burrower.

Pachydon hettneri (Anderson, 1928) and *Pachydon cebada* (Anderson, 1928) are found in Early Miocene deposits, preceding the major pachydontine radiations of the Middle Miocene. They are quite robust shallow diggers that lived in marginal lacustrine and lacustrine settings. *Pachydon hettneri* appears to be the shallower-living of the two species.

Pachydon iquitensis (de Greve, 1938) closely resembles *P. erectus*, but is thinner shelled, consistently smaller and more elongate. The range of morphological variation is large and possibly *P. iquitensis* yields several cryptic species (Wesselingh, 2006). The somewhat wrinkled shells are rostrate. The point of maximum density is located on the anterior half, indicating them to be top-down burrowers. The species is found in marginal to offshore lacustrine environments.

Two *Ostomya* species, *O. papyria* Conrad, 1871, and *O. carinata* Wesselingh, 2006, are rather thin-shelled, flat species that preferentially occur in lacustrine assemblages. Their ecological requirements are unclear. The pallial sinus is truncated, indicating a shallow burrowing behaviour.

Anticorbula mencheri (Palmer, 1945) is a very rare constituent of the upper (late Middle to early Late Miocene) parts of the Pebas Formation. It occurs in a sample that yields lacustrine, marginal lacustrine and fluvial taxa. The species was hitherto only known from the Pliocene Las Piedras Formation of eastern Venezuela, where it was found *in situ* in a fluvial assemblage (Palmer, 1945; own observations). *Anticorbula miocaenica* Wesselingh, 2006, is known from marginal lacustrine and fluvial assemblages of the Pebas Formation. It has also been encountered in samples from the Early Miocene Chaguaramas Formation of eastern Venezuela (Academy of Natural Sciences collections, pers. obs.). Both *Anticorbula* species are rare in the Pebas Formation. They are bilobed, but have more regularly developed shells than the extant *Anticorbula fluviatilis* (Adams, 1860; Amazon River, tributaries, rivers and upper estuaries in Guyanas; Nuttall, 1990; Leistikow & Janssen, 1997 as *Guianadesma sinuosum*). *Anticorbula fluviatilis* is an epibyssate nestler. Possibly, the fossil *A. mencheri* and *A. miocaenica* were infaunal as well as semi-infaunal.

Pachyrotunda rotundata Wesselingh, 2006, is a rather thin-shelled, circular and convex species that resembles in general outline the marine genus *Diplodonta*. *Pachyrotunda* is uncommon in the Pebas fauna, where it is found mainly in lacustrine assemblages. Its ecology is not understood.

Ecological explanations for the abundance of Pachydontinae in the Pebas system

What can explain the sheer abundance of pachydontine bivalves in the Pebas fauna? If the system was brackish, why are common marginal marine taxa lacking? On the other hand, if the system was fresh, why are corbiculids, sphaeriids and, to a lesser extent, unionoids so rare? Four possible reasons for the dominance of the Pachydontinae are explored.

Anomalohaline conditions – The conflicting views of salinity regimes in the Pebas system might appear to point to anomalohaline settings. Ichnofossil assemblages, for example, indicated mesohaline and oligohaline conditions as well as water stratification to be common in the Pebas system (Gingras *et al.*, 2002). However, the Pachydontinae appear very well adapted to fresh water settings as a group, despite the general (marginal) marine nature of the family to which they belong (Wesselingh *et al.,* 2002, 2006b). In the North American Paleogene, pachydontine clams co-occurred with strict freshwater viviparoid and unionoid species (Belt *et al.,* 2005). The single extant pachydontine species, *Anticorbula fluviatilis*, is known from the upper reaches of the Guyana estuaries,

possibly experiencing freshwater-mesohaline salinity variations, but the same species has also been recorded from Amazon floodplain lakes in central Brazil, possibly even up to Peruvian Amazonia, at least 2500 km and possibly even 4000 km away from marine influence (Pilsbry, 1944; Nuttall, 1990; Leistikow & Janssen, 1997; own observations). Based on faunal (Wesselingh *et al.,* 2002) and strontium isotope (Vonhof *et al.,* 1998, 2003) data I interpret the Pebas system, apart from small incursion levels actually yielding oligohaline faunas (Vermeij & Wesselingh, 2002; van Aartsen & Wesselingh, 2000), to be essentially a freshwater system. Negative $\delta^{18}O$ values (typically between -4 and -8‰) found throughout Pebasian bivalves rule out the possibility of an isolated brackish sea under arid climatic settings like the Caspian Sea (Wesselingh *et al.,* 2002; Kaandorp *et al.,* 2006). The predominantly freshwater nature of the Pebas system explains the absence of widespread marginal marine taxa such as oysters, mussels, mangrove cerithoideans, *etc.,* but leaves the question open why the Pachydontinae were so dominant over ordinary freshwater mussels such as unionoids and corbiculids.

High predation pressure – Several of the morphological characteristics of the Pachydontinae are interpretable in terms of adaptation against very high, marine-like predation intensities. The Pebas system abounded with molluscivore predators as shown by their fossil remains, as well as predation scars and common sharply edged shell fragments. Major molluscivore groups identified from the Pebas Formation are sciaeniid, myliobatiform and serrasalmine fishes (Monsch, 1998), and decapod crustaceans. Presumably other molluscivore predators, such as waterfowl, crocodiles and otters, were also present. Thick shells commonly observed in the Pebasian pachydontines can deter predation. However, in several species, such as *P. obliquus* and *P. carinatus*, selective shell thickening was found at the anterior margin, the area most difficult to reach for predators. These cannot be explained as an antipredatory adaptation. Several *Pachydon* species, including *P. trigonalis* and *P. cuneatus*, have strong postero-dorsal shell margins that may deter predation. The posterodorsal keels seen in other species (e.g., *P. carinatus, P. ledaeformis*) contribute to stronger shells. Predation scars are often observed on the posterior parts of pachydontine shells, indicating a predominant beak-down living position. The extreme convex nature of *P. obliquus* may also have helped deterring cracking type of predation (Fig. 1h, i). Other potential antipredatory traits in pachydontine bivalves include thickened ventral margins (common), valve overlap (common), the development of a rostrum protecting siphons (seen in varying extents in several species, with the most extreme case *P. ledaeformis*) and vacation of the interior marginal areas as indicated by the deep location of the pallial line in most pachydontines. However, these features may also have evolved for reasons other then as a response to intense predation. Finally, a suit of adaptations in all corbulid bivalves (including pachydontines) for hermetic sealing (complex interlocking hinge; inaequivalve condition with LV fitting into a groove of the RV and the seal being improved by the internal 'outcrop' of the main conchiolin layer) may also have been beneficial in deterring recognition from predators (Harper, 1994).

Adaptation to living in soft substrate – Corbulids have very short siphons reflecting a shallow burrowing life style. The non-streamlined, inflated morphology limits their ability to move through the sediment, so they are slow and cumbersome burrowers.

As a result they are highly prone to predation, and dislodgement by currents and bioturbation (Lewy & Samtleben, 1979). Many of the Pebas pachydontine corbulids are found in organic-rich mudstones that presumably formed fluid bottoms during deposition. Several works have dealt with adaptations of bivalves and other organisms to living in soft substrates (Stanley, 1970; Thayer, 1975; Savazzi, 1999). Various characters seen in the pachydontine bivalves indicate them to be very well adapted to fluid substrates, despite their in general large and heavy shells. The selective thickening of the anterior margin seen in, for example, *P. obliquus* and *P. carinatus* stabilized these shells in the soft substrate beak-down, thus ensuring the siphons to be close to the surface. This seems closely analogous to the living habit reconstructed for Mesozoic megalodontid bivalves (Skelton, 1978). A broad concave anterior platform on which *P. erectus* could balance provided a floating surface that may have circumvented the sinking of the bivalve. Reduction of shell size in muddy lacustrine bottoms (seen in, e.g., *P. trigonalis, P. obliquus* and *P. amazonensis*) enhanced floating capacity (Stanley, 1970). Oblique/lateral burrowing in *P. telliniformis* created a snowshoe effect (Thayer, 1975). The gryphaeid cup form of *Exallocorbula dispar* possibly also circumvented sinking. The large valve overlap at the ventral-anterior half possibly served as a protection against mud entering when the shell was opened. Extreme thinning and flattening of shells did reduce effective weight in *Concentricavalva concentrica*, although the role of its massive hinge plate is not well understood. The common presence in low abundances of epibyssate *Mytilopsis* shows that hard substrates, possibly in the form of dead shells, were available in the Pebas system, but as a whole the Pachydontinae appear to have developed a wide array of strategies coping with fluid substrate types.

Coping with dysoxia – The prevalence of blue organic-rich clays, as well as the common preservation of organic tissue such as periostracum, points to common dysoxia or anoxia within the bottoms of lakes in the Pebas system (Wesselingh *et al.,* 2006b). Oxygen stress was also indicated by specific recurring ichnofossil assemblages (Gingras *et al.,* 2002). A number of marine corbulids are well known to tolerate episodic low oxygen levels (Lewy & Samtleben, 1979; Harper, 1994). They can seal their valves and await the end of such unfavorable conditions, or can lower their metabolic rates, diminishing oxygen consumption. Several morphological characteristics in Pebasian pachydontines indicate the possibility of very tight closure, such as the receiving furrow in various of the pachydontine species, the complex interlocking hinge structures (most pronounced in *P. obliquus*), as well as a curved commissural plane. Possible cessation or lowering of metabolic rates might explain the generally rather irregular growth line successions, commonly seen in these bivalves (and often seriously complicating age estimates). *Exallocorbula dispar* and possibly *Pachydon amazonensis* may have developed a chemosymbiontic lifestyle. Possibly (facultative) chemosymbiosis was more widespread in the pachydontinae. Several of the species discussed above have a general morphology that indicates inefficient burrowing behaviour. This implies that *Pachydon* in general lived in little agitated environments, both physical and biological (low burrowing intensities). The presence of a very thin oxygenated zone, at best, in the bottom does explain a paucity of deeper burrowing benthos that could dislodge these shells.

Comparisons with other faunas

Some general characteristics of the Pachydontinae of the Pebas system resemble those of two other bivalve groups from Paratethyan long-lived lakes of Eastern Europe. Several radiations of lymnocardiids and to a lesser degree dreissenid bivalves occurred in Miocene Lake Pannon, Mio-Pliocene Euxinian Lakes, Pliocene Lake Aktchagyll and the Quaternary Caspian Sea (Danukalova, 1996; Müller *et al.,* 1999; Nevesskaja *et al.,* 2001). Although the continuity of evolutionary lineages from lake to lake are not agreed upon (see Nevesskaja *et al.,* 2001, and Grigorovich *et al.,* 2003, for conflicting views), the points in common between the two groups and the Pebasian Pachydontinae can be summarized as follows:

High species numbers (compared to related taxa in marine and fluvial faunas).

High endemicity rates.

Morphological variation exceeding that of closely related taxa in non-long-lived lake environments.

Ecological tolerances exceeding those of closely related taxa in non-long-lived lake environments, developing both specialists and secondary opportunists (Harzhauser & Mandic, 2004).

Therefore, the Pebasian Pachydontinae can be considered as typical representatives of long-lived lake groups. Long-lived lake bivalves show repeatedly the evolution of ecological tolerances and morphological characteristics that exceed the range of variation of their families in ordinary (non-long-lived) environments. These include expanded tolerance of salinity regimes (Pannonian, Euxinian, Aktschagylian and Caspian cardioids, Aktschagylian mactraids), expansion into fluid substrates (Aktschagylian and Pannonian cardiids) or lowered oxygen conditions (Pebasian *Exallocorbula* and Pannonian *Congeria*). The term "supralimital evolution", introduced by Myers (1960, p. 327) for this phenomenon in cyprinoid fishes in Lake Lanao (Philippines), should be used for this feature.

Evolution beyond usual tolerances and characters in long-lived lake taxa implies that reconstructing palaeoecological conditions using strict uniformitarian principles with these taxa is hazardous. More general reservations about the application of uniformitarianism in the geological record in general have been put forward by several authors, including Bottjer *et al.* (1995), Vermeij & Dudley (1985) and Vermeij (1987). These authors stress the need for the simultaneous use of independent faunal, geochemical and sedimentary criteria to reconstruct past ecological settings. For example, applying uniformitarianism to the predominant (endemic) corbulids led Nuttall (1990) and others to the interpretation of predominant brackish settings in the Pebas system, where the presence of unionoids and the absence of typical oligo- and mesohaline mollusc taxa, as well as strontium and stable oxygen isotope analyses, clearly indicated predominant fresh water conditions (Vonhof *et al.,* 1998, 2003; Wesselingh *et al.,* 2002).

Why, then, are freshwater groups so uncommon in the Pebas Formation? Cosmopolitan freshwater bivalve groups diversify very rarely in long-lived lakes and yield rather modest radiations only (unionoids in the Pannonian, Euxinian, Biwa and East African lakes, sphaeriids in Lake Baikal: Wesselingh, in press). This pattern is neither entirely appreciated nor fully understood. In the case of the Pebas system one can speculate about the poor representation of three groups of bivalves that lived in rivers

emptying into the lake; Corbiculidae, Unionoidea and Sphaeriidae. Corbiculids are restricted to (warm-)temperate and tropical settings. They favour well-oxygenated waters and appear to be intolerant to lowered oxygen settings. Such settings can be very widespread in tropical long-lived lakes, as a result of water stratification or high organic decomposition rates that intoxicate the bottom (Thayer, 1975; Stanley, 1970). There are plenty of indications for common oxygen stress in the Pebas Formation (Gingras *et al.*, 2002; Wesselingh *et al.*, 2002, 2006b; Kaandorp *et al.*, 2006), explaining the paucity of *Corbicula* in the Pebas fauna, despite its common occurrence in rivers and lakes in adjacent areas (Nuttall, 1990; Wesselingh, 2006). Some unionoids can tolerate lowered oxygen settings. Savazzi & Peiyi (1992) provided examples of morphological adaptations to dysoxia, as well as likely chemosymbiosis in some Chinese unionoids. However, most unionoids need well-oxygenated waters. Thus, oxygen stress, together with a combination of very high predation pressure and soft substrates, may have prevented them from becoming very abundant in the Pebas fauna. Sphaeriids might have floated in liquid mud, as a result of their small size, but are very easy targets for predators. These small clams also face difficulties in dealing with prolonged oxygen stress. Therefore, the predominance of Pachydontinae in the Pebas system is probably the result of their successful ability to deal with soft substrates, oxygen stress and possibly high predation intensities at the same time, thereby excluding common widespread non-marine bivalve groups.

Conclusions

The Pachydontinae from the Miocene Pebas Formation of western Amazonia are a species-rich group with a broad range of morphologies that reflect a number of living modes. These bivalves lived in a long-lived system of shallow lakes, where dysoxia was common. Their ability to deal with oxygen stress, soft substrates and high levels of predation permitted them to out-compete other non-marine taxa. Their uninterrupted presence throughout the Pebas Formation is indicative of the permanent presence of lacustrine aquatic habitats in the Pebas system. Pachydontinae do not occur in contemporary fluvial deposits, with the exception of *Anticorbula* species. The Pachydontinae waned with the termination of the Pebas system, *c*. 9 Ma ago, only to leave one lineage of *Anticorbula* to endure until today.

Acknowledgements

dam) about the depositional settings of the Pebas system. Through engaging discussions with Laurie Anderson (University of Louisiana, Baton Rouge) my understanding of the Corbulidae has drastically improved and she also critically read the original review. Willem Renema (Nationaal Natuurhistorisch Museum, Leiden) was flexible to allow me to use part of Wesselingh (in press) to include in this paper. Peter Skelton (The Open University, Milton Keynes) and Arie Janssen (Xewkija, Malta) provided helpful suggestions that improved the manuscript.

References

Aartsen, J.J. van & Wesselingh, F.P. 2000. New *Odostomia* species (Gastropoda, Heterobranchia, Pyramidellidae) from the Miocene Pebas Formation of western Amazonia (Peru, Colombia). *Basteria*, **64**: 163-168.

Adams, H. 1860. Description of a new genus of freshwater bivalve Mollusca, belonging to the family Corbulidae, from the collection of Hugh Cuming, Esq. *Proceedings of the zoological Society, London*, **28**: 203.

Anderson, F.M. 1928. Notes on Lower Tertiary deposits of Colombia and their molluscan and foraminiferal fauna. *Proceedings of the California Academy of Sciences*, **17**: 1-28.

Anderson, L.C., Hartman, J.H. & Wesselingh, F.P. 2006. Close evolutionary affinities between freshwater corbulid bivalves from the Neogene of western Amazonia and Paleogene of the northern Great Plains, USA. *Journal of South American Earth Sciences*, **21**: 28-48.

Belt, E.S., Tibert, N.E., Curran, H.A., Diemer, J.A., Hartman, J.H., Kroeger, T.J. & Harwood, D.M. 2005. Evidence for marine influence on a low-gradient coastal plain; ichnology and invertebrate paleontology of the lower Tongue River Member (Fort Union Formation, middle Paleocene), western Williston Basin, U.S.A. *Rocky Mountain Geology*, **40**: 1-24.

Bottjer, D.A., Campbell, K.A., Schubert, J.K. & Droser, M.L. 1995. Palaeoecological models, non-uniformitarianism, and tracking the changing ecology of the past. *In*: Bosence, D.W.J. & Allison, P.A. (eds.), *Marine Palaeoenvironmental Analysis from Fossils.* Geological Society Special Publication, **83**: 7-26.

Conrad, T.A. 1871. Descriptions of new fossil shells of the upper Amazon. *American Journal of Conchology*, **6**: 192-198.

Conrad, T.A. 1874. Remarks on the Tertiary clay of the Upper Amazon with descriptions of new shells. *Proceedings of the Academy of natural Sciences, Philadelphia*, **1874**: 25-32.

Dall, W.H. 1872. Note on the genus *Anisothyris*, Conrad, with a description of a new species. *American Journal of Conchology*, 7: 89-92.

Dall, W.H. 1898. Contributions to the Tertiary fauna of Florida with especial reference to the Silex beds of Tampa and the Pliocene beds of the Caloosahatchie River, including in many cases a complete revision of the generic groups treated of and their American Tertiary species. *Transactions of the Wagner Free Institute of Science of Philadelphia*, **3**: 571-947.

Danukalova, G. 1996. Bivalvian molluscs and stratigraphy of the Aktchagilian. *Trudy Palaeontogischeskih Instituta Rossia Akademyia Nauka*, **265**: 1-132. [In Russian.]

Gabb, W.M., 1869. Descriptions of fossils from the clay deposits of the Upper Amazon. *American Journal of Conchology*, **4**: 197-200.

Gingras, M.K., Räsänen, M.E., Pemberton, S.G. & Romero, L.P. 2002. Ichnology and sedimentology reveal depositional characteristics of bay-margin parasequences in the Miocene Amazonian foreland basin. *Journal of Sedimentary Research*, **72**: 871-883.

Greve, L. de. 1938. Eine Molluskenfauna aus dem Neogen von Iquitos am Oberen Amazonas in Peru. *Abhandlungen der Schweizerischen Palaeontologischen Gesellschaft*, **61**: 1-133.

Grigorovich, I.A., Therriaul, T.W. & MacIsaac, H.J. 2003. History of aquatic invertebrate invasions in the Caspian Sea. *Biological Invasions*, **5**: 103-115.

Harper, E.M. 1994. Are conchiolin sheets in corbulids bivalves primarily defensive? *Palaeontology*, **37**: 551-578.

Harzhauser, M. & Mandic, O. 2004. The muddy bottom of Lake Pannon – a challenge for dreissenid settlement (Late Miocene; Bivalvia). *Palaeogeography, Palaeoclimatology, Palaeoecology,* **204**: 331-352.

Hoorn, C. 1993. Marine incursions and the influence of Andean tectonics on the Miocene depositional history of northwestern Amazonia: results of a palynostratigraphic study. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **112**: 187-238.

Kaandorp, R. J. G., Vonhof, H.B., Wesselingh, F.P., Romero Pittman, L., Kroon, D. & Hinte, J.E. van. 2005. Seasonal Amazonian rainfall variation in the Miocene climate optimum. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **221**: 1-6.

Kaandorp, R., Wesselingh F. & Vonhof, H. 2006. Ecological implications from stable isotope records of Miocene western Amazonian bivalves. *Journal of South American Earth Sciences,* **21**: 54-74.

Lamarck, J.B.P. de. 1818. *Histoire naturelle des animaux sans vertèbres. 5.* Verdère, Paris: 1-612.

Leistikow, A. & Janssen, R. 1997. A record of the bivalve *Guianadesma sinuosum* Morrison from the central Amazon basin (Bivalvia, Corbulidae). *Basteria*, **61**: 17-22.

Lewy, Z. & Samtleben, C. 1979. Functional morphology and palaeontological significance of the conchiolin layers in corbulid pelecypods. *Lethaia*, **12**: 341-351.

Monsch, K.A. 1998. Miocene fish faunas from the northwestern Amazonia basin (Colombia, Peru, Brazil) with evidence of marine incursions. *Palaeogeography, Palaeoclimatology, Palaeoecology,* **143**: 31-50

Müller, P., Geary, D.H. & Magyar, I. 1999. The endemic molluscs of Late Miocene Lake Pannon: their origin, evolution and family-level taxonomy. *Lethaia*, **32**: 47-60

Muñoz-Torres, F., Whatley, R. & Harten, D. van. 1998. The endemic non-marine Miocene ostracod fauna of the Upper Amazon Basin. *Revista Española de Micropaleontologia*, **30**: 89-105.

Muñoz-Torres, F., Whatley, R.C. & Harten, D. van. 2006. Miocene ostracod (Crustacea) biostratigraphy of the Upper Amazon Basin and evolution of *Cyprideis*. *Journal of South American Earth Sciences*, **21**: 75-86.

Myers, G.S. 1960. The endemic fish fauna of Lake Lanao and the evolution of higher taxonomic categories. *Evolution*, **14**: 323-333.

Nemésio, A., Aronowsky, A. & Anderson, L.C. 2006 (in press). *Exallocorbula* (Bivalvia: Corbulidae), a new name for the Amazonian molluscan fossil *Pebasia* Nuttall. *The Veliger*.

Nevesskaja, L.A., Paramonova, N.P. & Popov, S.V. 2001. History of the Lymnocardiinae (Bivalvia, Cardiidae). *Paleontological Journal*, **35**: s147-s217.

Nuttall, C.P. 1990. A review of the Tertiary non-marine molluscan faunas of the Pebasian and other inland basins of north-western South America. *Bulletin of the British Museum (Natural History),* Geology, **45**: 165-371.

Oschmann, W. 1994. Adaptive pathways of benthic organisms in marine oxygen-controlled environments. *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, **191**: 393-444.

Palmer, K.v.W. 1945. Fossil fresh-water Mollusca from the State of Monagas, Venezuela. *Bulletins of American Paleontology*, **31**: 1-34.

Pilsbry, H.A. 1944. Molluscan fossils from the Rio Pachitea and vicinity in eastern Peru. *Proceedings of the Academy of natural Sciences, Philadelphia*, **46**: 137-153.

Räsänen, M.E., Linna, A., Irion, G., Rebata Hernani, L., Vargas Huaman, R. & Wesselingh, F. 1998. Geologia y geoformas de la zona de Iquitos. *Anales Turkuensis, (***AII) 114**: 59-137.

Salle, M.W. la & Cruz, A.A. de la. 1985. Species profiles: life histories and environmental requirements of coastal fisheries and invertebrates (Gulf of Mexico): common rangia. *Biological Report*, **82**: 1-29. Report can be downloaded from response.restoration.noaa.gov/cpr/watershed/calcasieu/calc_html/pdfs/sp_profiles/rangia-1.pdf.

Savazzi, E. 1999. Soft-bottom dwellers and the leaning tower of Pisa: adaptive exploitations of unstable positions. *In*: Savazzi, E. (ed.), *Functional Morphology of the Invertebrate Skeleton*: 123-128. Wiley, Chichester.

Savazzi, E. & Peiyi, Y. 1992. Some morphological adaptations in freshwater bivalves. *Lethaia*, **25**: 195-209.

Skelton, P.W. 1978. The evolution of functional design in rudists (Hippuritacea) and its taxonomic implications. *Philosophical Transactions of the Royal Society London*, **B284**: 305-318.

Stanley, S.M. 1970. Relation of shell form to life habits of the Bivalvia (Mollusca). *Geological Society of America Memoir*, **125**: 1-296.

Taylor, J.D. & Glover, E.A. 2000. Functional anatomy, chemosymbiosis and evolution of Lucinidae. *Geological Society Special Publications*, **177**: 207-225.

Thayer, C.W. 1975. Morphological adaptations of benthic invertebrates to soft substrata. *Journal of Marine Research*, **33**: 177-189.

Vermeij, G.J. 1987. *Evolution and Escalation: An Ecological History of Life*. Princeton University Press, Princeton, New Jersey: 527 pp.

Vermeij, G.J. & Dudley, E.C. 1985. Distributions of adaptations: a comparison between functional shell morphology of freshwater and marine pelecypods. *In*: Trueman, E.R. (ed.), *Biology of the Mollusca, Vol. 10, Evolution*. Academic Press, London: 461-478.

Vermeij, G.J. & Wesselingh, F.P. 2002. Neogastropod molluscs from the Miocene of western Amazonia, with comments on marine to freshwater transitions in mollusks. *Journal of Paleontology*, **76**: 265-270.

Vokes, H.E. 1945. Supraspecific groups of the pelecypod family Corbulidae. *American Museum of Natural History, Bulletin*, **86**: 5-32.

Vonhof, H.B., Wesselingh, F.P. & Ganssen, G.M. 1998. Reconstruction of the Miocene western Amazonian aquatic system using molluscan isotope signatures. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **141**: 85-93.

Vonhof, H.B., Wesselingh, F.P., Kaandorp, R.J.G., Davies, G.R., Hinte, J.E. van, Guerrero, G., Räsänen, M.E., Romero-Pitmann, L. & Ranzi, A. 2003. Paleogeography of Miocene Western Amazonia: isotopic composition of molluscan shells constrains the influence of marine incursions. *Geological Society of America Bulletin*, **115**: 983-993.

Wesselingh, F.P. 2006. Molluscs from the Miocene Pebas Formation of Peruvian and Colombian Amazonia. *Scripta Geologica*, **133**: 19-290.

Wesselingh, F.P. (in press). Long-lived lake molluscs as island faunas: a bivalve perspective. *In*: Renema, W. (ed.). Springer, Dordrecht.

Wesselingh, F.P., Hoorn, M.C., Guerrero, J., Räsänen, M.E., Romero Pittmann L. & Salo, J. 2006a. The stratigraphy and regional structure of Miocene deposits in western Amazonia (Peru, Colombia and Brazil), with implications for late Neogene landscape evolution. *Scripta Geologica*, **133**: 291-322.

Wesselingh, F.P., Kaandorp, R.J.G., Vonhof, H.B., Räsänen, M.E., Renema, W. & Gingras, M. 2006b. The nature of aquatic landscapes in the Miocene of western Amazonia: an integrated palaeontological and geochemical approach. *Scripta Geologica*, **133**: 363-393.

Wesselingh, F.P. & Macsotay, O. 2006. *Pachydon hettneri* (Anderson, 1928) as indicator for Caribbean-Amazonian lowland connections during the Early-Middle Miocene. *Journal of South American Earth Sciences*, **21:** 49-53.

Wesselingh, F.P., Ranzi, A. & Räsänen, M.E. 2006c. Miocene freshwater Mollusca from western Brazilian Amazonia. *Scripta Geologica*, **133**: 419-437.

Wesselingh, F.P., Räsänen, M.E., Irion, G., Vonhof, H.B., Kaandorp, R., Renema, W., Romero-Pittman, L. & Gingras, M. 2002. Lake Pebas: a palaeo-ecological reconstruction of a Miocene long-lived lake complex in western Amazonia. *Cainozoic Research*, **1**: 35-81.

Wesselingh, F.P., & Salo, J., 2006. A Miocene perspective on the evolution of the Amazonian biota. *Scripta Geologica*, **133**: 439-458.

Whatley, R., Muñoz-Torres, F. & Harten, D. van. 1998. Des ostracods d'un lac sale Néogène à l'ouest du basin Amazonien. *Proceedings of the Third European Symposium on Ostracoda, Bierville*: 25 pp.

Woodward, H., 1871. The Tertiary shells of the Amazons valley. *Annals and Magazine of Natural History, London*, **7**: 59-64, 101-109.