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Flying high: on the airborne dispersal of aquatic organisms as illustrated by the distribution histories of the gastropod genera *Tryonia* and *Planorbarius*

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Abstract

The actual and fossil distribution patterns of the aquatic gastropod genera *Tryonia* and *Planorbarius* indicate that avian dispersal was an important dispersal mechanism in the geological past. Combining the distribution histories of these genera with ecological data on modern relatives provides insights into the process of dispersal of aquatic taxa in general. Avian dispersal of aquatic taxa is facilitated by a variety of factors, including mass occurrence in resting/foraging places of migrating birds, ways to attach to the birds and to overcome desiccation during flight, as well as easy reproduction from a single specimen when introduced into a new habitat. The uncertain taxonomical status of aquatic organisms, as well as biased preservation and sampling, provide serious drawbacks for understanding the importance of aerial dispersal.

Introduction

Long-distance airborne dispersal has been used as an explanation for wide and discontinuous distribution ranges for a variety of biota. Migratory birds are thought to have provided the main mechanism for long-distance dispersal of plant species, e.g., for closely related plant species pairs that live in the temperate zones of North and South America but that are nearly or completely absent in between (Raven 1963). Terrestrial pulmonate snails of species from Puerto Rico and St Croix were found alive in the plumage of migrating birds shot in Arizona, U.S.A. and at Guantamo, Cuba (Ramsden 1914, Rees 1965). The appearance of (restricted) marine molluscan taxa, such as *Cerastoderma*, *Scrobicularia* and *Pirenella* in Saharan lakes, hundreds of kilometres from nearby seas, has also been attributed to long-distance dispersal through birds (Rose 1972, Spencer & Patchett 1997).

Aerial dispersal is much easier accomplished for terrestrial than for aquatic organisms, which have to overcome the problem of desiccation. How can, for example, the marine bivalve *Cerastoderma* have flown hundreds of kilometres inland into the Sahara, attached to a bird, without dying from desiccation?

In the present contribution we aim to address long-distance dispersal of aquatic organisms by air. We draw two examples from the fossil record: the distribution history of the neotropical gastropod genus *Tryonia* and of the Eurasian gastropod genus *Planorbarius*. The historical biogeography of these genera allows some general considerations on the aerial dispersal of aquatic organisms. The terms on which migratory birds may serve as an important agent for the dispersal of aquatic organisms are discussed.

Disjunct distribution and the role of birds

Disjunct distribution of organisms can be explained in three ways:

- the ancestral species was once widely distributed and the actual fragmentation of the distribution area is the result of subsequent development of barriers such as oceans, deserts or mountain ranges, the so-called vicariance model (Skelton 1993);
- by insufficient systematic knowledge: parallel evolution led to the development of closely similar morphospecies at distant locations (e.g. Gould 1985, for the terrestrial gastropod *Cerion*);
- the disjunct distribution is due to transport, the currently best known examples being due to accidental (unintentional) or purposeful introductions by man such as rats, goats and rabbits on islands, but many more examples can be found in the literature (Elton 1958, Hengeveld 1989).

Disjunct distributions, in particular those of freshwater snails and terrestrial snails, have often been explained by dispersal by birds. Lyell (1832) was one of the first to mention the possibility of transport by waterfowl to distant islands for a widely distributed land snail (*Succinea putris*) through the attachment of eggs to feathers (Lyell 1832, p. 109). He also raised the question whether eggs of land snails might be transported floating uninjured in seawater to distant shores. This suggestion was refuted by Darwin (1859) because adult freshwater snails and eggs are immediately killed by seawater. Baker (1945) showed that the flyways of migratory birds could nicely explain the distribution of freshwater planorbid snails over the West Indian islands, where the birds stop and rest en route. Gasse et al. (1987) suggested avian transport of marine organisms including the bivalves *Cerastoderma glaucum*, *Scrobicularia* sp. and the gastropod *Pirenella* sp. to inland brackish lakes in Northern Africa, located up to 500 km from the sea. For example, the salinity of Lake Birket Qarun, Egypt, increased from 1.1% to 2.8% between 1907 and 1987 and the above mentioned molluscs colonized the lake in this period, probably transported by birds (Rose 1972).

We can discern two ways in which birds can transport living molluscs: *internally* (in the digestive tract), or *externally*, attached to feathers or feet or in clay attached to the feet. The same holds for seeds of plants. In the past, more attention was paid to seed transport than to transport of molluscs, mainly to explain the occurrence of vegetation on remote islands (Ridley 1930, Raven 1963, Van der Pijl 1982). The population of remote or newly formed lakes has puzzled many scientists as well for over a century.

Most observations on transport by birds pertain to *external* transport. Darwin (1859, chapter XIII) observed ducks emerging from a pond with duckweed adhering to their backs. Eggs from which snails may emerge, may be attached to these duckweeds, as Darwin observed by introducing duckweed to aquaria. Darwin thought the feet of ducks more effective in transport, however, and for the purpose he suspended the feet of a duck in an aquarium with many hatching eggs of freshwater gastropods. The juvenile gastropods attached to the feet and could not easily be shaken off. They survived on the duck's feet in damp air from 12 to 20 hours. Similar experiments were conducted by Boag (1986), who allowed juvenile freshwater snails to adhere to feathers floating in an aquarium. Snails adhering to the feathers were subjected to a simulated flight in an air stream. He observed high loss rates in the gastropods by dying or falling off the feathers, but still his experiments indicated the probability of successful dispersal for distances up to 10 km.

External transport does occur in nature and was described by, among others, Roscoe (1955), who observed juvenile specimens of three freshwater gastropod genera, including the planorbid *Helisoma*, attached to the feathers of a white-faced ibis (*Plegadis chihi*). Rees (1965) gave more references, a.o. of numerous specimens of the freshwater gastropod *Physa* sp. found regularly on the migratory upland plover *Bartramia longicauda*, which carried ten to thirty snails under their wings upon arrival in Louisiana! This is remarkable, as this bird prefers dry areas (R. Dekker, pers. comm.).

Darwin (1878) also mentioned another possibility for external transport by birds: a living adult freshwater bivalve (*Unio complanatus*) was collected attached to the feet of a blue-winged teal (*Anas discors*). The living *Unio* had caught one of the teal's toes between its valves. Rees (1965, Table 4) lists a number of other examples of bivalves nipped on the toes of aquatic birds. This type of transport was described repeatedly for small bivalves nipped to the legs of water beetles, water scorpions or corixiids (see the references in Kew 1893, Rees 1965). Bondesen & Kaiser (1949) mentioned a comparable possibility for *Hydrobia jenkinsi* (= *Potamopyrgus antipodarum*) and other gastropods stening themselves to feathers by clenching them between operculum and shell. Ankel (1936) described this closure of the operculum as a reaction to predators, by which action the predator is sometimes caught between shell and operculum.

Observations of *internal* transport of molluscs by birds are few, whereas internal transport of viable seeds of plants is well documented (Ridley 1930, Raven 1963, Van der Pijl 1982). Also a number of viable small aquatic organisms or resting stages were reported to survive passage of the digestive tract of birds (Maguire 1963, Proctor & Malone 1965, Proctor et al. 1967, Atkinson 1972, 1980). In their exhaustive reviews of published data, neither Kew (1893) nor Rees (1965) reported records of molluscs surviving transit through the alimentary canal of birds. Later, Malone (1965a) experimented with two birds (mallard, *Anas platyrhynchos*, and killdeer, *Charadrius vociferus*) feeding them both snails and egg masses of which only a few eggs passed the digestive tract intact and developed normally to hatching. No juvenile or adult snails passed the gizzard, which leaves open the possibility of transport of intact molluscs in the crop before entering the gizzard (see also De Vlaming 1967). Indeed, Cadée (1995) mentioned a cockle, *Cerastoderma edule*, regurgitated alive by a herring gull and found in the act of burrowing again in the tidal flat. Mr P. de Wolf (NIOZ, pers. comm.) observed the same for living *Spisula subtruncata* clams from regurgitates of herring gulls on the North Sea beach of Texel in February 1998. Thompson & Sparks (1977) experimented with asiatic clams *Corbicula manilensis* fed to scaup ducks (*Aythya affinis*) and found no intact clams in the faeces. The clams had already died in the gizzard, probably due to a too high temperature. Mollusc-eating ducks and waders crush commonly all shells internally; this was reported for, among others, tufted duck (*Aythya fuligula*) and scaup (*Aythya marila*) (De Leeuw 1997), eider duck (*Somateria mollissima*) (Swennen 1976, Cadée 1994) and knot (*Calidris canutus*) (Dekinga & Piersma 1993). Cadée (1988, 1994) observed living *Hydrobia ulvae*, however, emerging from faeces of the shellduck (*Tadorna tadorna*), indicating that they survived the passage of the digestive tract. This seems an exception in birds crushing molluscs internally.

The numbers of *Hydrobia* observed alive in the shellduck' faeces were considerable: three droppings contained in total 140 living specimens and 960 empty and/or broken *Hydrobia* shells (Cadée 1988). They were, however, dropped on the same tidal flat the birds were feeding on, so transport distance was negligible. Such internal transport is probably always over short distances as the 'throughput' or 'retention' time for food (time between feeding and defecation) is only short. It is related to body size, because larger birds have longer digestive tracts (Bruinzeel et al. 1998). In, for instance, scaup, a bivalve-feeding duck with a body mass of 1300 g (comparable to that of the shellduck), throughput time was only 25 minutes (De Leeuw 1997).

With Malone (1965b), we suggest that external transport of molluscs by birds is more effective than internal transport. The distance travelled is longer and the survival rate is higher. Avian transport for aquatic biota is also more likely to be effective than wind-borne dispersal (see for examples Rees 1965) as wind-dispersal of aquatic biota will be more random, not directed to new aquatic environments (causing 'rains of fish' on land for instance) whereas migratory birds (waders, ducks) will fly from feeding area to feeding area along their flyway, as mentioned also by Baker (1945).

For dispersal by transport to be successful, the transported molluscs have to be able to propagate in the new environment. This will be easiest if they carry with them brood (internal brood-care, such as with *Tryonia*, detailed below) or if they are able to multiply parthenogenetically, as in, for instance, *Potamopyrgus antipodarum* (Cadée 1991). Also self-fertilization, occurring in hermaphrodite taxa such as *Planorbarius* (see below), enhances the possibilities of successful propagation (Baker 1945).

Transport of molluscs by birds over longer distances can occur only during migration. Migration between breeding and wintering areas occurs in many bird species, e.g., in 40% of the European bird species (Ricard 1969). Migration is no longer seen as related to the glacial period, but thought to have existed probably as long as birds themselves. It is seen as a naturally selected tendency of birds to live the year round in places where conditions are optimal for them (Welty 1982). Therefore migratory birds can also be used to explain pre-Pleistocene dispersal of molluscs.

The two examples treated below consider gastropods in the neotropics and in Europe. In Europe there are two main axes of bird migration: one NE–SW and one NW–SE; 150 species follow the first axis, of which 35 go as far as tropical Africa; 25 follow the second axis, of which 14 reach East Africa (Ricard 1969). The Mediterranean is an important obstacle, mainly crossed in the West (Gibraltar) and in the East (Bosporus), and the reason for the two European migration axes or flyways mentioned. North American

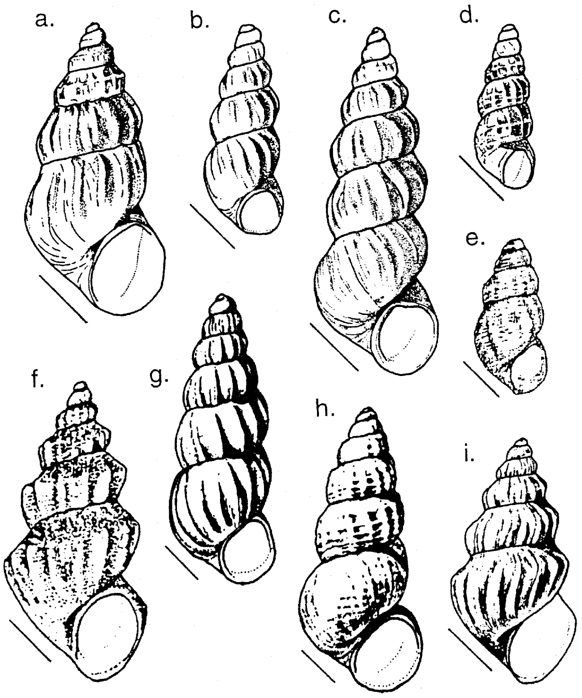

Figure 1. Range of morphological variation of fossil and modern *Tryonia* species. Scale bar 1 mm. a. *T. sp.*. b. *T. minuscula* (Gabb, 1869). c. *T. scalarioides* (Etheridge 1879). d. *T. cf. tuberculata* (de Greve, 1938), Miocene, Pebas Formation, Western Amazonia. e. *T.* sp.; extant, Cienaga Grande, Colombia (redrawn from von Cosel 1986, Figure 133). f. *T. guatemalensis* (Wesselingh 1996), Pliocene, Herreria Fm., Guatemala. g. *T. clathrata* Stimpson, 1865. h. *T. protea* (Gould 1855), extant, western interior, U.S.A. (redrawn from Burch 1989, Figures 133–134). i. *T. protea* (Gould 1855), extant, western interior, U.S.A. (redrawn from Burch 1989, Figures 136–137).

migrants do not encounter a comparable obstacle: they can circumvent the Gulf of Mexico either by flying across Mexico or by using West Indian islands as stepping stones. Some, however, take an Atlantic flyway crossing the ocean roughly from Labrador to the Guyanese or Brazilian coast (Ricard 1969, Welty 1982, Elphick 1995). Those migrants travelling long distances ($>$1000 km) nonstop and often over sea will do this in a short period of only days, but even this is probably a too long period for attached molluscs to survive. Those travelling over land or by island or wetland hopping will travel shorter times and distances and use good feeding areas on their way south or north to replenish fat stores. These wetland-hopping migrants are best suited for transporting externally attached molluscs.

Dispersal history of the genus Tryonia *Stimpson 1865*

Tryonia (Hydrobiidae: Cochliopinae) is an aquatic gastropod genus, species of which live in the western interior of the United States, Florida and in northern Guatemala (Hershler & Thompson 1992, Wesselingh et al. 1996). Species from the coastal zone of northern Colombia have been attributed to this genus as well. Fossil *Tryonia* species are known from the Pliocene of Guatemala and the Miocene of NW South America (Wesselingh et al. 1996).

Tryonia species inhabit lakes, streams, springs and lagoons. They live on soft bottoms, firm substrates and vegetation, and seem to prefer well-oxygenated waters (Taylor 1987). *Tryonia* feeds on algal ‘aufwuchs’ and on organic detritus. Species assigned to *Tryonia* have a range of salinity tolerances, from stenohaline freshwater to strongly euryhaline. Adults of *Tryonia* are small, with a shell height of commonly a few mm only. Females are ovoviviparous and have a brood sac that may contain few, variably sized, young (Hershler & Thompson 1992). Some of the currently living species exhibit clear sexual dimorphism (Taylor 1987), but this type of dimorphism has not yet been encountered in the fossil material. The systematic status (i.e. monophyly) of *Tryonia* is still subject of research. Assignment of all the fossils of this genus is purely based on shell morphology, which is a rather hazardous method, especially in hydrobiid snails. All the fossil material from central and South America, however, exhibits morphologies that are in a close range of morphological variation (Figure 1). Typically, *Tryonia* is elongate and bears well developed axial ribs. Spiral ribs occur occasionally, resulting in a reticulate sculpture. Smooth forms of *Tryonia* are found only in the northern end of its distribution (the western interior of the United States). The shell has a closed or narrowly rimate umbilicus, and the growth lines are usually prosocline.

Tryonia species were widely distributed in NW South America during the Miocene. During the Pliocene, *Tryonia* lived in Guatemala, north of the Panama corridor, whereas Quaternary/extant *Tryonia* species are known from the north coasts of Colombia and Venezuela, from Guatemala, Mexico, Florida, Texas and the western U.S. interior. The successive distribution ranges of *Tryonia* suggest a northward migration of the genus from the Miocene onward. This view cannot be conclusive, given the scarcity of appropriate fossil-bearing deposits in the neotropics.

The modern distribution of *Tryonia* is remarkably disjunct. Between the populations of Guatemala, Florida and the U.S. western interior, there are vast areas lacking species of *Tryonia*. Considering the density of collections from the region, it can almost be excluded that this pattern is the result of too little sampling of the 'barren' areas. Populations and species flocks of *Tryonia* are also disjunctly distributed within the Western interior. This is partly due to the aquatic habitats occurring very patchyly in this arid zone. On the other hand, *Tryonia* is found in many, isolated drainage systems and basins many of which cannot have been in mutual contact during the last five million years or so.

The fossil distribution of *Tryonia* also implies a patchy distribution in the past, although this pattern may well be a preservation artefact. Remarkable is that, whenever *Tryonia* occurs, it does so abundantly. *Tryonia* is lacking in places where the habitat would allow its presence: Pliocene and Quaternary inland lakes of northern Venezuela and Quaternary inland lakes in central America where species of the allied genera *Pyrgophorus* and *Mexipyrgus* occur(red) abundantly, in an ecological context apparently similar to that of *Tryonia*.

The fossil and modern distribution ranges of the various *Tryonia* species are all in areas along the routes of migratory waterfowl between North and South America. The distribution of *Tryonia* coincides, for example, almost completely with the present-day migration routes of the blue-winged teal (Figure 2). Distribution of *Tryonia* with the waterfowl would thus explain its distribution area as well as its disjunct occurrence. The migration routes of the blue-winged teal serve only as an example to illustrate migration routes of present-day waterfowl. *Tryonia* occurs in large numbers in shallow lakes, places where migratory waterfowl rest and forage. With high numbers of migratory birds visiting these places, the incidence of taking *Tryonia* is fairly high. If a single female specimen of *Tryonia* can be transported, it would be able to found a new population, as it can carry several young specimens in its brood-sack. Intermittent lakes in central America may provide important stepping stones for the dispersal of *Tryonia*. Avian dispersal and the dispersal pathways proposed for *Tryonia* are very similar to those described by Baker (1945) for tropical American planorbids.

Distribution history of Planorbarius *in Europe*

Planorbarius is a large planorbid genus living in Europe and Northern Asia. The only living European species, *P. corneus* (Linné), has an almost pan-European distribution. Large specimens occurring in the Balkan, attributed to *P. grandis* (Dunker), are considered to be a regional variety of *P. corneus*. *P. metidjensis* (Forbes) from the southern Iberian peninsula should be attributed to the genus *Bulinus* (E. Gittenberger, pers. comm.). *Planorbarius* belongs to the bassomatophoran lung snails. The species lives in stagnant fresh-water bodies, and has hardly been found in flowing waters (Janssen & De Vogel 1965, Gittenberger & Janssen 1998). It usually occurs in vegetated water bodies of some depth. *Planorbarius* is, like all planorbids, hermaphrodite. The oldest *Planorbarius* is known from upper Eocene deposits of Spain. Many species have been described from Miocene and younger deposits, and an extensive synonymy for fossil *Planorbarius* exists. In the present contribution,we discuss the occurrence of three species with a pan-European distribution pattern: *P. cornu* (Brogniart), *P. thiolierei* (Michaud) and *P. corneus*. Other species, restricted in time or distribution (e.g., *P. garsdorfensis* Schlickum and Strauch, *P. heriacensis* Fontannes) are not dealt with. The literature on the European species of *Planorbarius* was critically reviewed for the purpose. Only illustrated specimens were used and identified, as well as some material available from N. Greece, using criteria listed in Figure 3.

Two patterns emerge from the distribution history of the three *Planorbarius* species:

- new species appeared in the SW and E/SE ends of Europe and 'filled' the central parts of Europe later;
- ancient species persist in remote regions as relicts (*P. cornu* on Sardinia and *P. thiolierei* in the Kozani Basin, N. Greece).

The simultaneous appearance (in geological terms) of species in the SE and SW ends of Europe is remarkable. What kind of mechanism could have produced such a pattern? The disjunct appearance of *P. thiolierei* in the Early Pliocene may be explained by the Lago Mare phase at the end of the Miocene, when large parts of the Mediterranean consisted of inland lake basins (but see below). This cannot explain, however, the similar distribution pattern of early *P. corneus* in the Middle Pliocene. The fossil record in central and southern Europe appears to be sufficient to

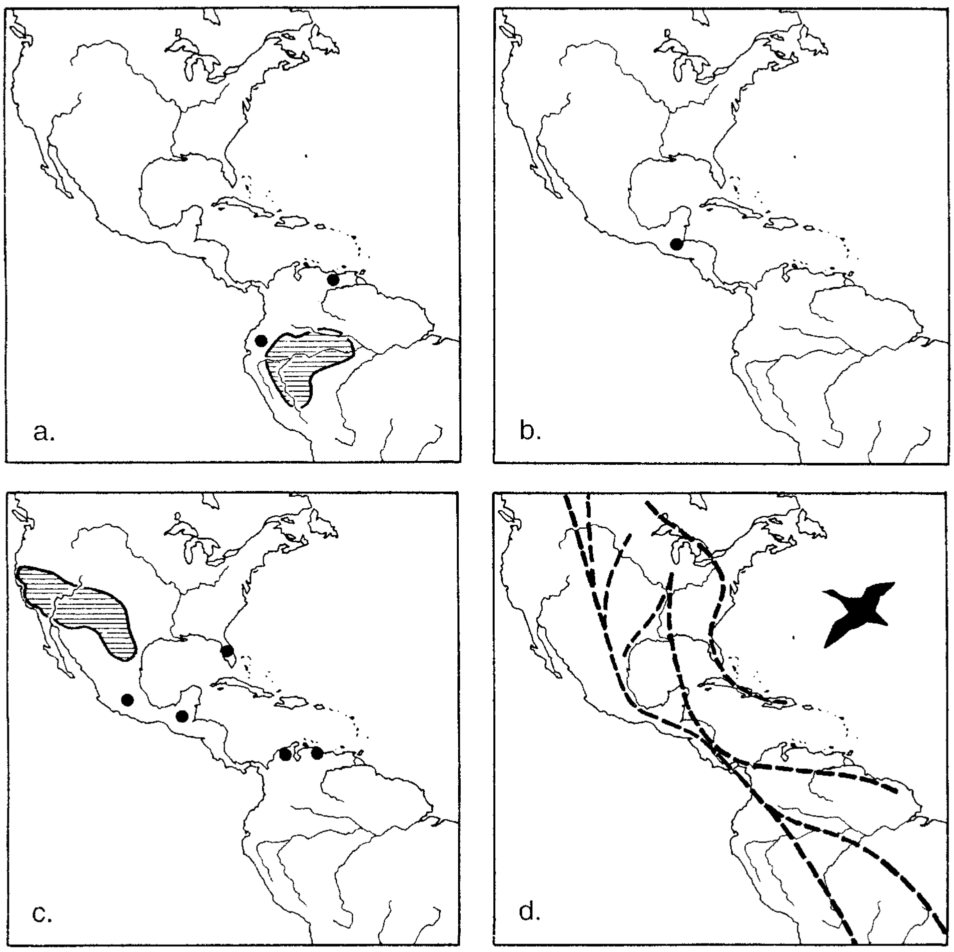

Figure 2. Distribution history of *Tryonia* a. Miocene. b. Pliocene. c. Quaternary/extant. d. Migration routes of the blue-winged teal. The migration routes of this bird (from Grosvenor 1979) are shown as an example to point to the co-incidence of migration routes of present-day waterfowl and the distribution of *Tryonia*. It is not known if the bird species already existed 3–5 Ma ago; if it did, it is unlikely that its migration routes were the same as nowadays. Apart from the blue-winged teal, other birds may have been responsible for the possible airborne dispersion of *Tryonia* as well.

rule out misinterpretations of the distribution areas of the various species. In northern Europe, however, and in particular in the lowlands of northern Germany, hardly any Neogene deposits containing fossil planorbids occur. The lack of fossils may therefore obscure the real distribution of *Planorbarius*. It cannot be excluded that species of *Planorbarius* emerged in northern Europe and spread from there to the SW and SE ends, to colonize central parts later.

Waterfowl live and forage in the same habitat where *Planorbarius* lives. Major migration routes at present are from Gibraltar (SW Europe) and from the Bosporus region (SE Europe) to Scandinavia and vice versa. We assume therefore that the Neogene distribution of a newly evolved species over Europe (Figure 4) was facilitated by transport by birds. To test the hypothesis of avian dispersal for *Planorbarius,* we should know whether inaccurate age-assignments may have led to the proposal of incorrect distribution patterns. The local stratigraphy of European inland regions (including those where fossil *Planorbarius* occurs) is rather complex, though units are usually attributed to one of four periods: Late Miocene (approx. 8 Ma), the Early (approx. 5 Ma), Middle (approx. 3.5 Ma) and Late Pliocene (approx. 2 Ma). The distribution patterns are therefore determined as accurate as these periods.

The flyways must have changed with palaeogeography and climates as well. Ancient migration routes are unknown, but can be deduced from palaeo-

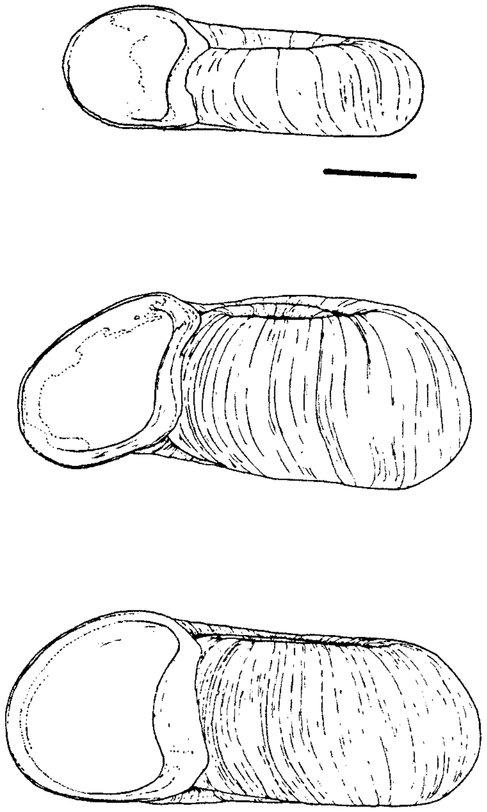

Figure 3. Distinction of *Planorbarius cornu, P. thiolierei* and *P. corneus*. Specimens housed in the Nationaal Natuurhistorisch Museum, Leiden, the Netherlands. Scale bar 5 mm. Top: *Planorbarius cornu* (Brogniart, 1810), which has a lower H/W ratio than the other two species. Whorls increase gradually, regular, but slowly in diameter and height. Aperture semicircular. RGM 221595 (Miocene, Saucats, Gironde dept., France). Middle:*Planorbarius thiolierei* (Michaud, 1851), which is larger and has a higher H/W ratio than *P. cornu*. Whorls increase irregularly in height and diameter. Prominently depressed dorsal apertural margin. Ventral apertural margin projecting downward. Aperture oblique. Subrounded keel on the basal periphery. RGM 394096 (Pliocene, Kozani, Greece). Bottom: *Planorbarius corneus* (Linné, 1767), which has a similar size and H/W ratio to *P. thiolierei*. The whorl diameter and height in *P. corneus* increase regularly. The dorsal apertural margin is subrounded, base of aperture not lowered. Periphery rounded. Aperture hoof-formed. NNM 1ax (Bois de Meudon, Paris, France).

geographical reconstructions. Modern N–S migration routes are very much determined by narrow cross-overs of seas. Nowadays, important cross-over points, where major N–S migration routes are channelled, are Gibraltar, the Bosporus and the western Baltic, through. During the Late Miocene, similar possibilities to cross the Mediterranean existed. The Arabian peninsula merged with Asia from the Early Miocene on, and the distance between northern Africa and Gibraltar was also short. Another possible land bridge was the N–S trending Italian peninsula, still in use as a N–S migration route by some birds (Elphick 1995).

Other ways to explain the distribution patterns of *Planorbarius* show serious drawbacks. *Planorbarius* doesn't tolerate salt water, making a range extension through sea impossible. Drainage reorganisations (such as by stream capture) may provide a way to extend the distribution area. In the Neogene, rather dramatical drainage re-organisations occurred in central Europe, but these cannot explain the observed pattern of initial distribution ranges of new species in the periphery of Europe.

Following the Messinian (latest Miocene) salinity crisis, the Mediterranean transformed briefly into a series of inland lakes that may have provided suitable habitats for continental and freshwater biota. This Lago Mare period ended with the opening of the Strait of Gibraltar. Lago Mare deposits contain, however, almost exclusively euryhaline tolerant biota, and lack planorbids. This may indicate that these waters did not provide suitable habitats for *Planorbarius* and thus should be excluded as an explanation for the disjunct Early Pliocene appearance of *P. thiolierei*. In the Kozani Basin (Greece), *P. cornu* was replaced by *P. thiolierei* some 0.1 Ma after the onset of the Pliocene (Steenbrink, pers. comm.). After the Miocene, the modern geographic configuration of Europe evolved. The Alps gradually reached their present altitudes and became hostile for both migratory birds and *Planorbarius*. The influence of climates on avian migration in the Neogene is unknown.

Can *Planorbarius* be transported by birds? *Planorbarius* species, in particular *P. corneus* and *P. thiolierei*, are rather large snails. Unlike some other planorbids (such as *Anisus* and *Planorbis*), *Planorbarius* does not survive very long when out of the water. Juveniles have a comparatively large aperture and a very thin shell, so they are probably even more prone to desiccation. It is therefore unlikely that the adults or juveniles can be carried alive by birds over a long distance, in agreement with observations by Boag (1986). The avian distribution of other planorbids along major migration routes in the Caribbean, as proposed by Baker (1945), implies that some desiccation resistance must be present in planorbids, which are able to colonize islands dozens to over a hundred of kilometres apart. *Planorbarius*, like all planorbids, lacks the operculum that may help to overcome drought. Eggs of *Planorbarius* are encapsuled in a jelly substance, protecting them from dehydration. These egg capsules are laid within shallow vegetation in which many birds forage. When some of these capsules become attached to the feet or the feathers of birds, the embryos may survive some time, to hatch after arrival in another area.

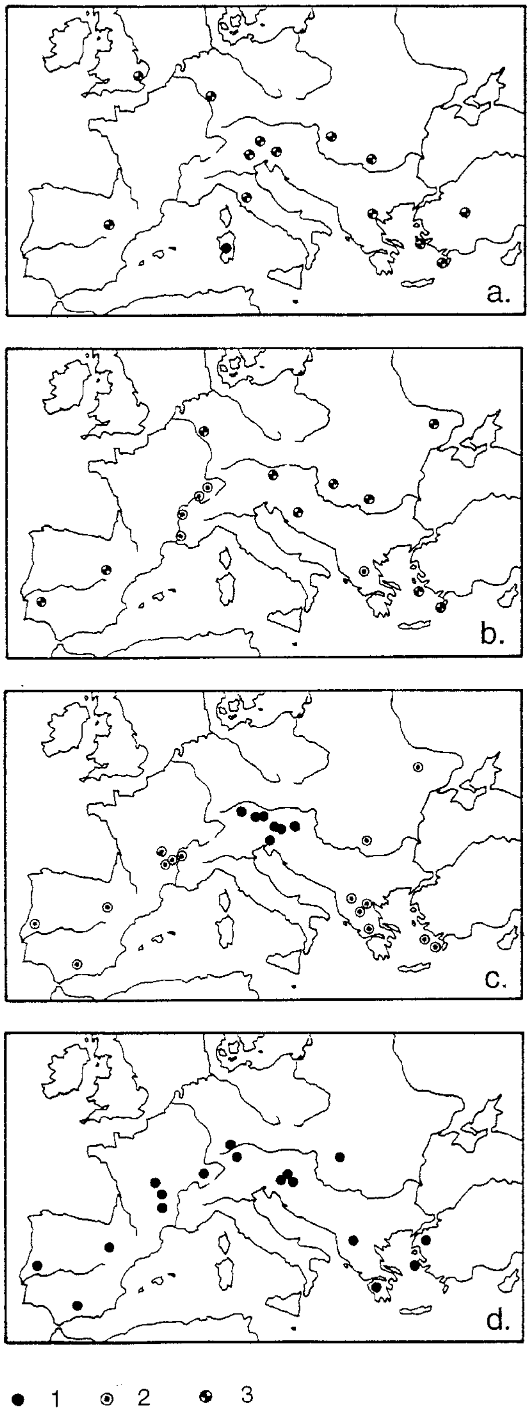

Figure 4. Neogene distribution of *Planorbarius*. (1 = *Planorbarius cornu*; 2 = *P. thiolierei*; 3 = *P. corneus*). a. Late Pliocene. b. Middle Pliocene. c. Early Pliocene. d. Late Miocene.

Conclusions

Aerial dispersal may be important as a means of distributional range enlargment for aquatic organisms. To be a potentially important mode of dispersion, the aquatic taxa must:

1. occur abundantly in areas where migratory birds rest and forage,
2. have the ability to clamp onto the host,
3. overcome dessication,
4. easily reproduce, ideally from a single individual, when encountering a new habitat.

The distribution histories of *Tryonia* and *Planorbarius* suggest avian dispersal. Both meet the requirements listed above: (1) the snails occur abundantly in habitats regularly visited by migratory birds, (2) attachment to birds feet may occur by egg capsules (for *Planorbarius*), (3) dessication may be overcome by the operculum (*Tryonia*) or by egg capsules (*Planorbarius*), and (4) both (may) propagate from a single individual: *Tryonia* females may bear several young with them, and *Planorbarius* is a hermaphrodite.

Aerial transport appears most likely to take place in the form of eggs or juveniles clamped onto birds' feet, in or without mud. Moreover, small adult individuals may survive transport clamped onto birds' feet: *Tryonia* specimens are usually a few mm only. It is unlikely that large adult snails adhering to birds feet, or their transport through the digestive track, will contribute significantly to long-distance dispersal. The presence of stepping stones on the migration routes, such as lakes, is also important to successful aerial dispersal.

Interpretation of aerial dispersal may be swamped by uncertainties in the taxonomical status of the taxa. Reconstructing dispersal histories must take into account former geographical configurations and corresponding bird-migration routes, as well as the incomplete nature of the fossil record and possible stratigraphical errors.

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