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The Dahomey Gap as evidenced by land molluscs, a preliminary report resulting from a reconnaissance of the literature[1]

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A survey of the pertinent literature has shown that the Dahomey Gap, a major interval in the West African forest block, is indeed a significant biogeographical barrier for land molluscs. The West African forest has been reduced to four refugia 18,000 years BP, subsequently merging into the western (Upper Guinea) and eastern (Lower Guinea) divisions of this forest belt. This vicariance event must have considerably influenced the distribution of terrestrial gastropods. From the literature it appears that insufficient data are yet available to draw conclusions. Our knowledge of the phylogeny (particularly sister-group relationships) of most groups is still in its infancy, although there are strong indications that much of the local endemism has originated in the four refugia.

Key words: Gastropoda, terrestrial Prosobranchia, Pulmonata, biogeography, phylogeny, vicariance, refugia, West Africa, Dahomey Gap.

The dominant feature of the vegetation in Africa today is the tropical forest belt surrounded by the savanna zone. Most of the land molluscs are concentrated in the forest and its sometimes strikingly isolated outliers. Man is encroaching upon the edges of the forest, but one has to realize that these margins have never been permanent boundaries. Throughout the chequered climatic history of Africa the forest has waxed and alternatively waned in its relation with the rainfall and the adjoining savanna. The central body of the great forest realm is not entirely continuous and the most conspicuous gap is the interval in West Africa, usually termed the Dahomey Gap (or Togo-Dahomey Gap), here abbreviated DG. This, one of the lesser biogeographical features, nevertheless has acquired some fame of its own, recently mainly because of a controversy as regards its significance for distribution patterns of plants and animals. Indeed, some flatly deny its existence, or rather its biogeographical importance as such, and argue that the Niger River instead is a biogeographical barrier of much greater interest.

The DG as it manifests itself today as an ecogeographical barrier to forest animals is roughly situated between Ghana in the west and Nigeria in the east, covering the political units of Togo and Dahomey inclusive of parts of western Nigeria (fig. 1). The width is slightly more than 300 km, but, although parts of the gap are fairly arid, there is intermittent forest in a woodland-savanna mosaic pattern.

A scrutiny of the past of the forest in West Africa reveals that in an arid or interpluvial period c. 18,000 years BP the forest block was mainly reduced to four major refugia (see e.g., Diamond & Hamilton, 1980; Hamilton, 1981; Van Zinderen Bakker, 1982). From west to east these were located at (1) Cape Palmas (on the

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[1] Paper read at the Ninth International Malacological Congress, Edinburgh, 1986. Outside pressure has supplied the incentive to withdraw the paper from the congress proceedings so that quicker publication may be achieved.

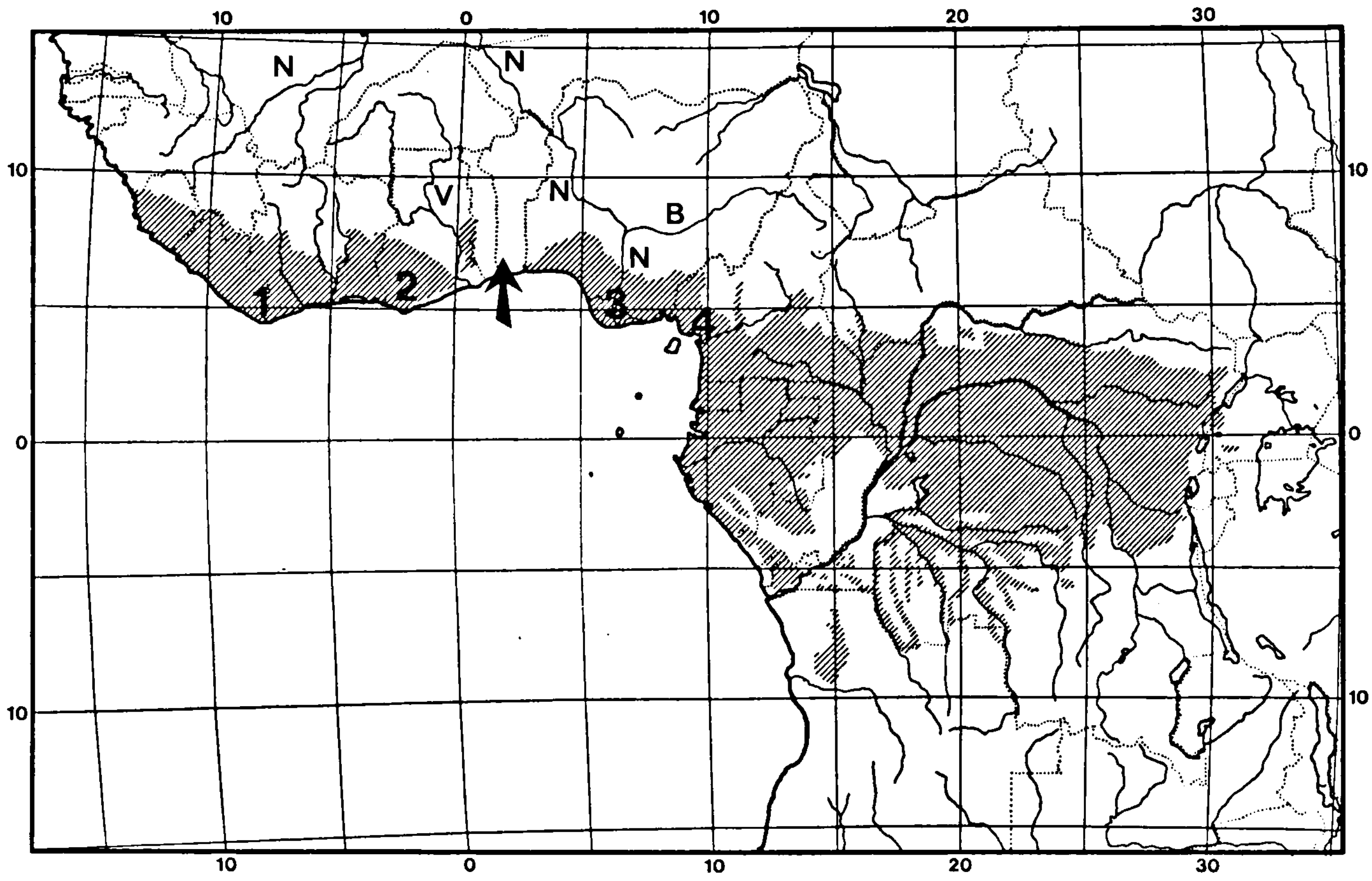

Fig. 1. The West African forest block (cross-hatched). The arrow indicates the Dahomey Gap, 1-4 the forest refugia 18,000 years BP (1 + 2 now forming the Upper Guinea, 3 + 4 the Lower Guinea forest blocks). Some major rivers have been indicated, B = Benue, N = Niger, V = Volta River.

borders of Liberia and Ivory Coast), (2) Cape Three Points (SE. Ivory Coast and SW. Ghana), (3) the Niger River delta (Calabar in Nigeria), and (4) coastal Cameroon s.l. A once continuous forest belt therefore became fragmented; when the rainfall once again increased considerably, the four refugia subsequently merged two by two into (a) the Upper (areas 1 plus 2) and (b) the Lower (areas 3 plus 4) Guinea forest blocks, thereby leaving a vacuum in the form of the present DG. It is not clear whether once again one uninterrupted block was formed, before a final division into two components. The scenario here adopted is that the four refugia formed the two present components without such a prior merger. Obviously many animals and plants did not cross the Niger River from their original place of retirement, although the forest once more expanded west of this major barrier.

The critical and comprehensive paper by Robbins (1978) examines the DG and its significance for high forest mammal distribution. Robbins reviews the various opinions and shows that "the Dahomey Gap has not influenced mammal distribution or evolutionary changes. Rather it is the Volta and Niger rivers, which have affected mammalian distribution and speciation in West Africa." (Summary on p. 168). From this it is clear that we have here a purely semantic problem. The name 'Dahomey Gap' is indeed strictly incorrect, but the fact that there is a gap of considerable biogeographical importance cannot be denied. For convenience's sake we propose to retain the wrong name when discussing the major interval in the West African forest belt.

Land molluscs are excellent material for biogeographical studies (cf. Solem & Van Bruggen, 1984). It is expected that the forest refugia of about 18,000 years BP will have influenced present-day distributions patterns of terrestrial snails in West Africa[2]. The fragmentation of the Guinea forest belt may be considered a classical vicariance event. The consequences of this division are the following potential modern distribution patterns:

(1) Occurrence throughout the forest in West Africa (taxa with wide original distribution not apparently affected by what has happened in the past).

(2) Occurrence of (pairs of) sister taxa on both sides of the interval (vicariant evolution).

(3) Occurrence of certain taxa on either side of the interval, implying selective extinction of the sister taxa on the other side.

(4) Occurrence of certain taxa on either side of the interval, implying dispersal to, but not beyond, the boundaries of the interval. Of course, one may expect less clear-cut cases exhibiting a mixture of some of the above patterns, as the case may be.

There is a lot of literature on the terrestrial molluscs of West Africa, but widely scattered and far from comprehensive. Some crucial areas have hardly been covered and unfortunately there are no modern check-lists or collations. A first and modest endeavour by Binder (1981) should be mentioned here. What is needed is good monographic work and local check-lists with proper distribution data; otherwise phylogenetic implications cannot be traced. All this has resulted in a severely restricted number of potentially useful papers relevant to the present problem. The results are

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[2] The distribution of freshwater molluscs is usually dependent on the history of river and lake systems. The arid phase must have had some influence on these systems, so that the DG perhaps is of significance to this group of molluscs as well. Brown (1980) shows four prosobranch gastropod genera (all monotypic) to be restricted to the area west of the DG (*Afropomus, Saulea, Soapitia, Sierraia*), while species of e.g., *Pseudocleopatra* display allopatric patterns on both sides of the DG.

also generally disappointing. The various groups on which data are available are treated below in systematic order.

The Afrotropical Region is singularly poor in terrestrial operculates. Few extend their distribution as far west as Upper Guinea. Only the genus *Maizaniella* (Maizaniidae, see Van Bruggen, 1982) is represented west of the DG, viz., by the monotypic subgenus *Maizaniella* s.s. and a species of the subgenus *Spirulozania*. The latter subgenus is also widely distributed in the Lower Guinea forest block; the species may also occur east of the DG. Unfortunately it is as yet well-nigh impossible to unravel sister group relationships in this case.

Only five species of the primitive and aberrant slug family Veronicellidae occur west of the DG, of which two also east of that interval (Forcart, 1953). The three endemics are *Pseudoveronicella (Hoffmannia) pauliani* Forcart, 1953, *P.* (*Vaginina*) *conradti* (Simroth, 1913), and *P.* (*V.*) *duporti* Forcart, 1953. The first species has its closest allies on both sides of the DG. The subgenus *Vaginina* (bar one species of unknown provenance) is endemic to the Upper Guinea forest; it is clearly an offshoot of *Pseudoveronicella* s.s. (probably the sister group), which inhabits much of West and Central Africa (inclusive of the far western districts). Therefore, the Veronicellidae hardly display significant vicariance patterns as regards the DG.

The Subulinidae, the sister group of the Achatinidae, encompass 34 genera/subgenera in Africa (Zilch, 1959); 15 of these occur in West Africa, and of these again six are endemic to this area. However, examination of available data shows that at the most two genera/subgenera are endemic to the Upper Guinea forest, *Striosubulina* (however, also on the Gulf of Guinea islands, i.e. effectively east of the DG) and *Neoglessula*. Furthermore the systematics of the family leaves a lot to be desired, so that it is better to wait for modern and comprehensive data before considering potential influence of the DG on this group.

The Achatinidae as a group are fairly well known and some data for certain groups have been extracted from the literature. From a total of 23 genera/subgenera nine are endemic to West Africa; a total of six (among which four of the endemics) occur west of the DG (see table 1; cf. Van Bruggen, 1986). There are no taxa on the genus/subgenus level restricted to the Upper Guinea forest. However, as shown in table 1 a number of taxa on this level does not overcome the DG.

On the species level there is an interesting taxon in the genus *Limicolaria* (data ex Crowley & Pain, 1970). This is *L. rohlfsi* Kobelt, 1894, which is restricted to possibly a forest refugium on the junction of the Niger and Benue Rivers beyond the past and present limits of the forest in Nigeria. It appears to be allied to two other species which (together with another two) are widely distributed in West Africa on both sides of the DG, occurring as far west as Ghana, Guinea and Senegal.

The species of two subgenera of *Archachatina* display patterns relevant to the DG (all data ex Bequaert, 1950). The subgenus *Calachatina* consists of five species (see table 2). One of these is widely distributed east of the DG, viz., from Dahomey to Central Africa, *A.* (*C.*) *marginata* (Swainson, 1821); its closest ally, *A.*(*C.*) *gaboonensis* Pilsbry, 1933, is much more restricted in its distribution, but does not cross the DG. The remaining three species are fairly closely related inter se. *A.* (*C.*) *ventricosa* (Gould, 1850), *A.* (*C.*) *degneri* Bequart & Clench, 1936, and *A.* (*C.*) *rhodostoma* (Philippi, 1849), are all restricted to west of the DG. This complex looks like exhibiting a vicariant sister group pattern as compared to the other two beyond the interval.

The other subgenus, *Megachatinopsis*, also encompasses five species, which relevant to the DG display strictly allopatric patterns (table 2). *A.* (*M.*) *knorri* (Jonas, 1839), *A.* (*M.*) *siderata* (Reeve, 1849), and *A.* (*M.*) *purpurea* (Gmelin, 1790) are restricted to

WEST OF DAHOMEY GAP	EAST OF DAHOMEY GAP
—	*Achatina* (*Tripachatina*)
—	*Achatina* (*Leptocala*)
Archachatina (*Archachatina*)	*Archachatina* (*Archachatina*)
Archachatina (*Calachatina*)	*Archachatina* (*Calachatina*)
Archachatina (*Megachatinopsis*)	*Archachatina* (*Megachatinopsis*)
—	*Columna*
—	*Pseudachatina*
—	*Atopocochlis*
Lignus	*Lignus*

Table 1. Nine genera/subgenera of Achatinidae are endemic to West Africa. Some of these do not cross the Dahomey Gap; the column on the left lists the taxa occurring on both sides of the Dahomey Gap.

west of the DG, while the other two, *A.* (*M.*) *papyracea* (Pfeiffer, 1845) and *A.* (*M.*) *camerunensis* (d'Ailly, 1896), only occur east of this interval. Incidentally, the former is known from Cameroon westward as far west as the Niger delta, i.e., does not cross this major river.

Finally, in what formerly was called *Callistoplepa* (a composite genus), there may be interesting patterns; the relationships of the various taxa are still under review (Prof. A. R. Mead, Tucson, personal communication).

Considerable though these achatinid data may seem, there appear to be no distinct vicariant pairs or other apparent sister-group relationships. This is mainly due to lack of knowledge of the relationships of the taxa involved rather than absence of sufficient

Archachatina, subgenus *Calachatina*	
WEST OF DAHOMEY GAP	EAST OF DAHOMEY GAP
A. (*C.*) *ventricosa*	*A.* (*C.*) *gaboonensis*
degneri	*marginata*
rhodostoma	

Archachatina, subgenus *Megachatinopsis*	
WEST OF DAHOMEY GAP	EAST OF DAHOMEY GAP
A. (*M.*) *knorri*	*A.* (*M.*) *papyracea*
siderata	*camerunensis*
purpurea	

Table 2. Distribution of the species of two subgenera of *Archachatina* (Achatinidae) endemic to West Africa (data ex Bequaert, 1950). As far as known, no species in these taxa occur on both sides of the DG.

distribution data. Our knowledge of the phylogeny in the Achatinidae is virtually nil; although a lot of anatomical evidence is available (much of it not yet published, we still have to rely on Mead's first pioneering paper (1950). The above limited biogeographical data make one speculate that all groups unknown west of the DG must have either become extinct there or are such recent developments that they have never crossed the DG (or for that matter the Niger River). Data as regards *Atopocochlis* in Mead (1950) support the latter contention. In addition, *Archachatina* (*Calachatina*) *marginata* and *A.* (*C.*) *degneri* may be sister species, exhibiting completely allopatric distributions, the former just about east, the latter only west of the DG. Would this be an example of vicariant speciation in separate refugia? Attention should be focussed on the allopatric complexes in both *Calachatina* and *Megachatinopsis* where vicariant phylogenetic grouping seems most likely.

The family Streptaxidae, one of the most diverse in Africa, is represented by numerous taxa in the West African forest belt. On the generic/subgeneric level there are surprisingly few streptaxids confined to the Upper Guinea forest. On a total of 46 genera/subgenera in the Afrotropical Region (Zilch, 1960), probably only four (with a low total diversity of under ten species) are endemic to this forest block. These may be *Artemonopsis* (subgenus of *Tayloria*, monotypic), *Lamelliger* (syn. *Odontartemon*, with at most three species), *Ptychotrema* s.s. (monotypic), and *Adjua* (subgenus of *Ptychotrema*, with three species). Only *Artemonopsis* looks like a product of long-standing isolation; its closest allies all occur in Central/East Africa — one might even suggest it to be the sister group of all other *Tayloria*. However, this has no implications as regards the DG. On the specific level there are many taxa that are restricted to the Upper Guinea forest, particularly in the genus *Gulella*. Many of the subgenera of this very diverse taxon may display allopatric specific distributions with respect to the DG, e.g., *Digulella* and *Paucidentella*. Endemism in the Upper Guinea forest is striking. One example should suffice. Binder (1963) in enumerating the molluscs of Mt. Nimba in Guinea lists 13 species of Streptaxidae of which six *Gulella*. These are all endemic to the area west of the DG; the remaining seven consist of five *Gonaxis*, one *Edentulina* and one *Ptychotrema*, only the last two not endemic. Thus, of 13 streptaxids 11 are indeed endemic! This paper lists a total of 31 species of land molluscs, 18 of which or 58% are restricted to the Upper Guinea forest. Unfortunately data on the phylogeny of the Streptaxidae are lacking altogether, which makes further discussion futile. We may only conclude that this family includes a host of potentially crucial cases for tracing the influence of climatic changes in the past in West Africa.

The Urocyclidae, another family endemic to the Afrotropical Region, permit evaluation of some data because of the existence of two recent monographic reviews (Van Mol, 1970; Van Goethem, 1977). Van Mol's treatise shows very characteristic allopatric patterns as regards the DG. *Senegalarion*, *Granularion*, *Amatarion*, and *Sylvarion* all occur only west of the DG, while all other genera are either confined to the area east of the DG or are distributed elsewhere in Africa. There are no genera known to occur all over West Africa s.l., i.e. on both sides of the interval under discussion. The monotypic genus *Senegalarion* seems to be related to an Ethiopian genus. *Granularion* (with ten species) and *Amatarion* (monotypic) are closely related and possibly sister groups. The likewise monotypic genus *Sylvarion* may have as its sister group slug-like genera such as *Estria* and *Dendrolimax* (see below).

Van Goethem (1977) has treated the slugs in the family, generally considered the most highly evolved urocyclids. Four genera appear to be confined to west of the DG, *Tresia*, *Estria*, *Aspidotomium*, and *Aspidelus*. *Microcyclus* occurs on either side of the DG. The widely distributed genus *Dendrolimax* exhibits some peculiar (artificial, because of insufficient sampling?) patterns; the species are clustered just west of the DG (Ghana and Togo), east of the DG (western Cameroon), on the islands of the Gulf of Guinea, and in Central, Central/East and southern Africa. There is definitely an allopatric pattern as regards the DG, but unfortunately too few data are yet available. The four western endemic genera are closely related; a suggested arrangement might be as follows — *Estria* and *Aspidotomium* are sister groups and both together form the sister group of *Tresia*, while *Aspidelus* remains a genus inquirendum in a phylogenetical sense. The complex of four genera might have the allopatric *Rhopalogonium*/*Varania* (Cameroon) complex as its sister group. Together this then looks like a pattern of vicariant evolution resulting from the erstwhile fragmentation of the West African forest belt. The case of *Dendrolimax*, isolated in the tribe Dendrolimacini, is a different one; this genus is probably only remotely allied to the other slug genera, having as its possible sister group a complex with considerably less reduced shells.

Another African endemic family, the Gymnarionidae (probably the sister group of the Urocyclidae), might possibly in the future supply interesting data. A paper by Binder (1976) describes a total of 11 species of *Gymnarion* all confined to the Upper Guinea forest block. In this genus most species are known to occupy sometimes very restricted ranges and comparable data for the Lower Guinea forest, i.e. east of the DG, are not yet available. This is certainly a case where a search for the sister groups would be most rewarding.

From the above limited exposé it is clear that there is an abundance of suitable distribution patterns. Obviously there is a minority of land mollusc taxa that exhibit overall West African distributions; most are restricted to either the Upper or the Lower Guinea forest and research on their relationships now seems imperative. Also, much more data are needed for a meaningful evaluation of the DG in connection with land snails. Field work on both sides of the dry interval, i.e. in south-eastern Ghana/south-western Togo and south-eastern Dahomey/south-western Nigeria, is essential. In addition the forest patches in the DG, if still extant, should be carefully sampled; data on mammals and birds in this area are of great biogeographical interest. Also, following Robbins' conclusions (1978), the position of the Volta and Niger Rivers as barriers rather than the DG proper, should be investigated.

Note added after completion of the manuscript

After the manuscript was submitted early in September 1986, two major publications relevant to the subject became available, Happold (1987) and Mayr & O'Hara (1986). Both supply background material supporting the preliminary conclusions of the present author's paper, but are based on results pertaining to groups much better collected and researched than land molluscs, i.e. mammals and birds. Special attention is drawn to table 15.3 on p. 249 (mammal species east and west of the Niger River), pp. 292-295 and fig. 18.3 in Happold (1987).

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