

# Saurologica

No. 7

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The Wall Lizards of the Upper Mainz Basin, Germany,  
with a look at the dispersal restraints for allochthonous wall lizards

Köln / Cologne

1.IX.2020

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with a look at the dispersal restraints for allochthonous wall lizards

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## 1. Some thoughts on clades and subspecies of the Common Wall Lizard

The Common Wall Lizard has a wide range north of the Mediterranean Sea. It has survived the Ice Ages of the Pleistocene in warm refugia and since spread into its current distribution. During isolation in the refugia, the genetic structure has evolved individual traits which are detectable with modern tools of genetic analysis (Harris & Arnold 1999). Animals with specific genetic traits are grouped in the so-called clades. Animals of a certain clade share their difference towards other groups. However, the modifications of the wall lizards seem not to have reached the cellular nucleus (nuclear DNA) but rather affected only the mitochondrial genome (mtDNA) which is determined by the mothers only, leaving out any effect from the father's side. After each Ice Age, the lizards have spread from their refugium into the warmed-up territory, where they finally mixed and interbred with specimens of other clades. It may be assumed that a "clean" clade may only have persisted in or close to its refugium, in the best case a refugium which remained the same for all Ice Ages, and the chances for such a situation have diminished with each Ice Age and subsequent warming.

In modern times, human influence has facilitated the mixing-up of the DNA, facilitated by the fact that the wall lizards are ideal stow-aways in plant and stone shipments: First, the spread of wine-growing, mainly due to the lack of equipment for water purification, brought an import of different wine plants into areas suitable for wine-growing, viz. warm areas with a potential for wall lizard habitats. Later, the building of churches and castles required the importation of stones, e.g. marbles from the Lahn valley to Cologne, stones from the Rhine drainage system to the Dutch coast for dam-building, marbles from Italy to Germany. The construction of railway tracks facilitated the movement of goods and provided corridors for natural expansion. Today, the exchange of agricultural goods and the release of specimens by amateurs are the main reasons for the establishment of new populations in warm places and the mixing of genes into existing populations.

A ground-breaking study (Schulte et al. 2008) identified four main clades (Western France, South Alps, Venetian, and Slovenian clades) as the origin of introductions into the indigenous German wall lizard populations, and subsequent authors have followed this analysis for other northern locations (Benelux, GB). Some introductions have built pure populations, while others have mixed with indigenous lizards and/or foreign lizards which have been imported earlier (Schulte et al. 2012). It is difficult to say whether hybridisations occurred pre- or post-importation (Michalides et al. 2015). Furthermore, the time needed for hybridisation may differ from case to case, be it because of differing habitat (Beninde & Feldmeier 2018) and ecological preferences (e.g. Börner 2020), be it because of inherent mating restraints like e.g. pheromone preferences (Perez i de Lanuza et al. 20018, 2019; Yang et al. 2018).

Later analyses over the total range of the Common Wall Lizard show the existence of at least 23 clades; they may be grouped into four main assemblages (Mayer & Schweiger 2011, Salvi et al. 2013), which are not identical with the four clades of the imports into Germany and neighbouring countries. Furthermore, the new study (Salvi et al. 2013) shows that the situation is complex even in the Mediterranean core range of the Common Wall Lizard, which is demonstrated not to be restricted to Italy alone, as was previously thought (Harris & Arnold 1999): There are clades that have spread and mixed with neighbours, as it could be expected for a warm period, and there are even populations of a certain clade outside its range, a situation which may be explained mainly by human interference, but maybe also by intra-specific competition.

## 2. The Eastern France clade

According to their mtDNA the indigenous Common Wall Lizards of the Rhine and Rhône valleys belong to the Eastern France clade.

The naming of subspecies (for names and synonymy see Mertens & Wermuth 1960) does not reflect the clades or their groupings. Rather, names were applied to lizard populations which seemed morphologically similar; this does not reflect phylogeny as it is required today. Instead of monophyletic units, sometimes ecomorphs and even paraphyletic units make up a subspecies. Apart from the island subspecies, there are plenty names for continental forms.

At present, the Eastern France clade has the name *Podarcis muralis brongniardii* (Daudin, 1802) due to its *terra typica* in Paris and the fact that it can be distinguished neither genetically nor morphologically from the subspecies *merremius* (Risso, 1826) with its *terra typica* Nice. The idea that the animals from the Maas valley differ from those of the Rhine valley (Gruschwitz & Böhme 1986, Schulte 2008) has not taken into account that there has been a continuous landscape throughout the ages until modern times, when the populations were separated by the (re-)growing of woods and the expansion and intensive use of agricultural lands. Accordingly, I have not detected any visual difference between all these animals.

Northern *Podarcis muralis brongniardii* show a colouration which is mainly basic for the species (for the variation along the Rhine see photos in Börner 2015 and figs. 4-15):

Basic colour of head and back is light shades of usually brown, sometimes grey; the ground colour may have a greenish tinge, which is mainly due to the reflection of sunlight (figs. 5-8), especially in freshly shed individuals. Rarely the basic colour it rarely is reddish (fig. 9) or even transparently or fully black.

Juveniles and females have whitish supraciliary stripes, usually as a strict line and rarely as a confluent sequence of light ocellae, and dark brown temporal bands running from the head all along the body and ending on the sides of the tail in alternating white and blackish transversal elements. Usually, along the body there is a whitish subocular line and sometimes below that a diffuse light brown line.

The black vertebral line is reduced in width and continuity, sometimes even absent.

Neonates have greyish tails for the last two-thirds of their length, which later turn light grey. Neonates and juveniles are plain white underneath.

The underside of adults is usually white, sometime reddish, sometime yellow. The colour indicates the state of immunity fitness (Sacchi et al. 2007). The red and yellow colours occur only in older, well-established populations. Adults, mostly males, may have blue or black outer ventral scales. Sometimes, there are a few small black spots on the throat, mostly in males.

Usually males and rarely females show a black, rarely bluish axillary ocella.

In males, the temporal stripe as well as an eventual vertebral line are dissolved into transversal bars and lines; they do not form a series of dark-rimmed ocellae. The dark elements are more prominent on the sides than on the back, where they tend to form a wormlike pattern, sometimes even confluent into a network.

Our domestic lizards are active even at low temperatures during spring and fall and avoid the high temperatures of noon and summer, mainly staying in their burrows or in the shade of the vegetation. They are found on stone, wood and even barren earth substrates, preferably south-faced and preferably, in case of lacking vertical structures, at least a little bit sloped. They

frequently visit trees (figs. 16, 17). If disturbed on walls or other vertical structures, they usually flee downwards into the vegetation.

The other clades differ slightly in outer morphology, but there is always considerable overlap in the populations (for details of the Western French and Northern Italian clades as well as hybrids in Mannheim see Deichsel & Schulte 2015). It does help to observe the populations in their natural surroundings, as you can see differences between the clades in habitat preference, temperature preference, activity periods, and behaviour (Börner 2015, 2020).

### 3. The Mainz Basin

The Upper Middle Rhine Valley (from Bingen to Koblenz) is a rift valley with slopes rising up to about 250 m on each bank, the most famous of which is the Loreley Rock (fig. 1). It is dominated by vineyards on the steep slopes of the Hunsrück Hills and the Taunus Hills.

The Upper Middle Rhine Valley is a major corridor for Mediterranean faunal and floral elements, which entered the Rhine Valley via the Burgundian Gate from the Rhône Valley towards the north, finally expanding into the Lower Middle Rhine Valley (from Koblenz to Bonn/Cologne) and into the Middle Rhine tributaries like Nahe, Wisper, Mosel, Lahn, Ahr etc. Among those Rhône elements, there is the Common Wall Lizard *Podarcis muralis* (Laurenti, 1768), which has developed sizeable populations in the hot, rocky slopes along the above-mentioned rivers and tributaries.

Upstream, the Rhine comes from the South, takes a bend to the West near Mainz and Wiesbaden to run through the Mainz Basin along the Rheingau, which lies on the northern bank, and then the Rhine turns North again at Bingen where the Upper Middle Rhine Valley starts (fig. 1)

Mainz lies basically on the south bank of the Rhine, but two suburbs (Kastel and Kostheim) are on the north bank. Wiesbaden is exclusively on the north bank. Today, Mainz is the capital of the State of Rhineland-Palatinate, and Wiesbaden is the capital of the State of Hessen in Germany. The area is so densely populated that the suburban sprawls meet easily in the gentle slopes and the riverine plains; in between there are only a few green patches of agricultural lands, to the west mainly orchards and the vineyards of the Rheingau and to the east mainly crop fields and pastures.

For the region around Mainz and Wiesbaden, historically no wall lizards have been reported in the old times (Mertens 1947). Heimes mentioned a population of introduced wall lizards near Wiesbaden in 1990, and the search has intensified after 2000 (Zitzmann et al. 2015).

There is a reason for this lack of indigenous wall lizards in the area:

The Mainz basin is a geological sink west of the Rhenanian city Mainz (fig. 2). On the south bank of the Rhine it extends to Bingen in the West; on the north bank it comprises of the sloping Wiesbaden plateau and extends to the gentle slopes of the Rheingau (fig. 3). In general, the sink lacks height differences greater than 20 m. It is bordered in the East by the Hunsrück Hills (250 m near the Rhine and up to 800 m at Erbeskopf)) and in the north the Taunus Hills (250 m near the Rhine, up to 600 m at the watershed and up to 800 m in the High Taunus). In the Mainz Basin, the Rhine has a number of flat islands and may be called "Island Rhine". Even after river dyking and flood management, the basin serves as a floodplain: Here the Rhine is usually about 400 m wide and may extend up to a width of 900 m during floods, which may originate from (1) the upper Rhine, (2) the Main which comes from the East and is

confluent at Mainz, and (3) the Nahe which comes from the West and is confluent at Bingen, where its high waters may back up. The Upper Middle Rhine Valley is too steep to allow for retention capacity, and the Rhine has to pass through the Loreley Gorge, which is only some 145 m wide. So the waters rise easily in the Mainz Basin and overflow the islands as well as the flat banks. At least before river containment measures the Mainz Basin has not provided a stable xeric, rocky environment as preferred by the Common Wall Lizard. Only anthropogenic structures like dams, walls, raised railway tracks and highways, quarries etc. provide for vertical elements which may collect the heat of the sun.

On the dams, the wall lizards avoid the area close to the water and visit it only briefly for chasing insects. While the sand lizard is known to survive winter flooding in its burrows, this is obviously not the case with the wall lizards. They hibernate out of the reach of the waters. Their occurrence is thus quite restricted in the Mainz Basin.

#### 4. The Common Wall Lizard on the South bank

##### a) The Bingen area

Bammerlin et al. (1996, p. 391) show a distribution map indicating Bingen as the southeasternmost point of the wall lizard distribution along the Rhine Valley; south of Bingen, there have been locality records only in the hill country (Haardttrand, Pfälzer Wald). This can be confirmed here as follows:

Typical Rhine Valley wall lizards are found on the Scharlachkopf of Bingen; the Scharlachkopf is just south of the mouth of the Nahe River and is the northern point of the Rochusberg. The southeasternmost point of occurrence of the wall lizards is in the north of Bingen-Gaulsheim (near former Hindenburg Railway Bridge, the pillars of which have no wall lizards), viz. in sight of the southern part of Rochusberg; these animals are typical *Podarcis muralis brongniardii*, Eastern France clade (figs. 18, 19). They are rare in the south-facing slopes of the heavily used railway tracks running south to Ingelheim, and already Gaulsheim railway station is without wall lizards.

To the East, towards Ingelheim and Mainz, the southern embankments of the Rhine are flat, and the pastures, orchards, and similar niches are occupied, if at all, by sand lizards and slow worms. The ferry point at Ingelheim-West is without wall lizards.

Like Fuhrmann et al. (2007), I have not found any wall lizards near Ingelheim, not even near the railway tracks, which cross the rather flat landscape (fig. 20). The Ingelheimer Aue is a meadowland near the Rhine which is unsuitable for wall lizards. This is not the "Ingelheimer Aue" mentioned by Fuhrmann et al. (2007) and Schulte & Deichsel (2015) (see the chapter on Mainz for further details).

Any wall lizard records from the area east of Bingen may be based on an occasional railway drop-off or, in case of the islands, an occasional release by users of the summer camping grounds. In the Mainz sink, there are no autochthous wall lizards east of Bingen.

##### b) Mainz- Budenheim

Schulte et al. (2008) list a population of wall lizards from the quarry at Budenheim and specifies that it is a relocation from Ilmenauer Aue; upon genetic examination of three specimens, he found that their mtDNA belongs exclusively to the Western France clade (see also Gassert et

al. 2013). This is repeated in part in his later listings, but then with a population estimate of 2.000+ individuals and a new interim origin: Ingelheimer Aue (Schulte & Deichsel 2015).

Research beyond the hospitalities rendered by the golf course management has revealed an opinion by Tauchert & Thiele of 2010, which states that from 2007 to 2009 more than 3.700 wall lizards have been relocated from Ilmenauer Aue and Ingelheimer Aue, areas with railway tracks in Mainz near the big freight harbour and in the industrial park; from the railway triangle Ilmenauer Aue extends about 1 km to the south with tracks running through the Gonsbach valley in Mainz. The western part of the industrial area is for the light industry, car dealerships and outlets, and this is now "Ingelheimer Aue" according to the traffic signs.

Today, the status of the Mainz-Budenheim hotspot, which carries the main population, is as follows:

The quarry has been transformed into a golf course. Its natural parts as well as artificially planted areas are densely populated with the wall lizards (figs. 21 et seq.), and the golf course warden has told me that this successful relocation is monitored closely.

In a new housing area west of the quarry the extant lizards have been removed, but today they are returning and are now found near Lennebergweg of eastern Mainz-Budenheim in parking lots, playgrounds, and gardens. There is a chance that the population will also expand to the East into a garbage center, another light industry park, surrounding bushlands, and allotment gardens.

Deichsel and Schulte (2015) say that the Western France clade is morphologically very close to the Eastern France clade, but may have a more intense and coarser colouration than the latter.

My photos confirm this, but also show that there are two basic forms of males, females, and juveniles, viz. a heavily coloured form with usually a rich dark brown basic colour and nearly black markings (figs. 23-25, 29) and a light, almost patternless ("buckskin") form with a light greyish-brown basic colour and dark grayish markings (figs. 26-28, 30). The brown ground colour lacks any tinge of grey, yellow, red, or green, as it may be found in the Eastern clade. The basic colour remains a walnut or hazelnut brown, while the Eastern clade tends to show a yellowish or reddish light brown ground colour. The pattern of the Western France clade is very close to that of the Eastern France clade. In the Western France clade, the most outstanding difference are one or more conspicuous axillary ocelli, usually with a black rim and a contrasting light, rarely black center; in the Eastern France clade, these ocellae, if present at all, are filled with black and rarely with blue or yellow. The light supralabial stripe of lizards of the Western France consists of a series of fairly large light (white or whitish) spots. Sometimes, the supraciliary stripe consists of a series of light, combined spots. The vertebral line is thin or broad, often only a series of dark spots. On the central back males have a black vermiculation pattern rather than a spotted pattern derived from ocellae; the transversal vermiculation will usually dissolve any vertebral lines or spots. The chin and the throat may have larger black spots. In their first days neonates have a light grey tail, which they keep.

Mainz-Budenheim has a small harbour which does not have wall lizards. However, due to the courtesy of Mrs. C. Kaiser I have been able to look for them at Kreuzer Hof, a small settlement facing the Rhine in a protected area in the East of Mainz-Budenheim and directly opposite to the entry of Schierstein harbour on the south bank of the Rhine (see Below). Kreuzer Hof has the wall lizard of the Western France clade (figs. 33-35), but only very few shy ones. They show the distinctive axillary ocellae. The male lizard, which I found, is quite dark and has blackish throat marks (fig. 29). The females have the contrasting stripes on the body and are

white underneath (figs. 30, 31). This is an isolated population which has been introduced either with garden materials or by pleasure boats.

c) Ilmenauer Aue and Mainz harbour

As mentioned above, the Mainz wall lizards relocated into the Budenheim quarry have come from the lower Gonsbach valley, called Ilmenauer Aue. Tauchert & Thiele (2010) state that despite the relocations some lizards may still have remained in their respective areas and others have been left undisturbed in the industrial park and in the Mainz harbour; both areas are situated on the bank of the Rhine, viz. northeast of Ilmenauer Aue.

I think that these wall lizards have been the first in the Mainz area. They seem to have arrived with ship freight and then spread along the rail tracks; in earlier times, the railtracks started at the harbour and were more in number and more heavily used. However, the lizards have not reached Mainz central station in the East and have not spread southwards beyond the railroad triangle into the Gonsbach valley due to a lack of suitable structures in this moist and tree-shaded valley. The sometimes terraced gardens of the classic villas on the south slope of the Gonsbach valley are on the Eastern side and are separated from the tracks by the creek and moist meadows; I have not found any wall lizard nor the smallest hint at their existence north of the sports grounds.

Today, their range consists of the freight harbour and the adjacent industrial park. It practically does not extend south of the throughway; too much heavy construction of new facilities is going on, and wastelands are rare.

aa) The area around the freight harbour consists of two parts: While the western part is dominated by industrial plants and a freight harbour and has remained basically unchanged, the eastern part with the pleasure boat harbour and its vicinity is under heavy reconstruction in favour of new high-class apartments and offices. In consequence, lizards can only be found in spots of the western part.

The freight harbour has a northern peninsula where the main development is the new central power and heat station for Mainz and Wiesbaden. It burns waste, and there are large deposits in the vicinity. These areas are without lizards.

The south-facing, harbour-facing dam of the peninsula has some lizards in unshaded, but vegetated areas (figs.34-35). The wall lizards are notably lighter and quite yellowish in their colouration (figs. 36-41) and smaller in size in comparison to those from the majority from the Budenheim quarry and its vicinity, but all show at least one distinctive dark-rimmed axillary ocella and the usual pattern of the Western France clade. The lizards may be smaller due to a scarcity of food and predation pressure from crows.

The freight harbour, where loads of building materials and timber have been received, is the most likely point of import for lizards of the French Atlantic coast. I think that the "buckskin" colouration type of Budenheim quarry is a secondary manifestation and may have its origin in this "light type" of colouration; if this is correct, it has ramifications on the origin of the "Elville-Walluf type" of the north bank, which is to be discussed below.

bb) In the industrial park, large areas are fenced off. I have found wall lizards at the foot of "Kaiserbrücke" which leads the railway tracks over the Rhine, and near its railway station "Mainz-Nord" (figs. 42- 47). Due to the continuous range, they should belong to *Podarcis muralis brongniardii*, Western France clade. They show the distinctive axillary ocellae, a brown

ground colour (no “buckskin” individuals), distinctive blackish markings, and most are white underneath, all that speaking for this classification. However, an influence by the lizards from the north bank of the Rhine cannot be excluded, especially when you look at the intensively dark and ocellated pattern of the male with the yellow throat (fig. 42). Those north bank lizards are highly invasive *Podarcis muralis cf. maculiventris*, and by railway they are less than two kilometers from Mainz-Nord railway station. If this is true, we see an invasion from the north, which has started to be successful at the point which is closest to the distribution of that population, and the start of a reduction of range of the pure Western France clade into the fringes of its current distribution.

## 5. The Common Wall Lizards of the North bank

### a) Rheingau

#### aa) Rüdeshheim

The area on the north shore from Rüdeshheim (opposite Bingen) to Wiesbaden is called the Rheingau (fig. 48). It is famous for its wines, and as there are stone walls to terrace the sloped terrain, healthy populations of the Common Wall Lizard can be expected (along with the Smooth Snake *Coronella austriaca* Laurenti, 1768, a live-bearing northern species feeding mainly on lizards, and the Aesculapian Snake *Zamenis I. longissimus* (Laurenti, 1768), an egg-laying Mediterranean species also preying reptiles). However, the wall lizard populations are thin and widely spread in the vineyards, mainly due to zoning and restructuring, the plastering of stone walls with concrete, as well as years of intensive spraying with biocides. A couple of hotspots remain, certainly at historic buildings (castles and wineries) and railway tracks (fig. 49); the southernmost extension of the typical *Podarcis muralis brongniardii*, Eastern France clade (fig. 50), reaches the railway tracks in Oestrich-Winkel and their vicinity (Börner 2015).

#### bb) Eltville and Walluf

A hotspot on the northern bank of the Rhine is the former towing path from Eltville (East) to Walluf (center) (fig. 51). As I have already noticed before I had seen the Western France clade of Mainz-Budenheim and the peculiar lizards of the Cyperus area, the lizards of the towing path look and behave differently than our typical Eastern France clade lizards.

The Eltville-Walluf lizards are restricted to the vertical wall and chase for prey in the vegetation at the bottom of the wall, from where they rarely cross the path into the dense vegetation directly along the river, as well as above the wall in the gardens. They like high temperatures and mostly flee upwards on the wall, even if they are in the lower part of it or even in the vegetation at its bottom. The lizards have not spread from the wall over the busy street into the railway tracks, which run parallel to the Rhine, or beyond into the hills, where there are gardens and vineyards. All of this is in contrast to the behaviour of our indigenous wall lizards.

The majority of Eltville-Walluf lizards (figs. 52-65) show an unconspicuously contrasted striped pattern, as it is usual for the Eastern and the Western France clades (figs. 52, 54-56, 58). There are dark individuals as well as very lightly-coloured ones (figs. 56, 57, 60), and most lizards show at least one dark axillary ocella, such characters speaking for the Western France clade. Almost all lizards flee upward when disturbed, only a few seek refuge in the ground vegetation and crevices. In contrast to this, only few adults reach the size typical for the

Western France clade, but this may be due to food scarcity in the confined wall habitat. However, some neonates have the darker tails, which are normal for the Eastern France clade, and some have the light grey tails which are normal in the Western France clade. And the lizards differ from the pure Western France clade in their temperature preference and related behaviour, which allows them to thrive even in somewhat shaded parts of the wall and aligns them with the Eastern France clade, too.

The lizards of the Cyperus and Hessler areas are completely different, as will be explained below.

Therefore, I suspect that the Eltville-Walluf lizards may be a hybrid of the Eastern and the Western France clades. As ca. 3.700 Western France clade lizards have been collected for relocation (Tauchert & Thiele 2005) and only 2.000+ individuals have made it into the Budenheim quarry (Schulte 2008, 2015), it seems probable that some of the missing ca. 1.500 lizards have been released in other supposedly suitable and easily accessible places. Some have perished (perhaps on the dams of the north bank like e.g. Ingelheim and Budenheim ferry points), some have barely survived (as e.g. at Kreuzer Hof gardens, if they did not arrive there by pleasure boat or with building materials and garden supplies), and some have flourished (as e.g. on the Eltville-Walluf wall). Such a development seems to be much more likely than an accidental rafting from the Mainz freight harbour through the obstacles of the islands in the Rhine, which deviate the current and do not provide a suitable habitat for wall lizards; the rafting alternative is even more unlikely in view of the yellow colouration of the outer freight harbour animals versus the predominantly dark colouration of the Eltville-Walluf lizards.

#### cc) Schierstein

Fuhrmann (2005) mentions the Wiesbaden suburb Schierstein (water works and harbour) as another locality for wall lizards, but has not found any.

The waterworks have a protected area in the "Schiersteiner Aue" (Schierstein meadowland) which extends along the Rhine between Walluf and Schierstein with a rather flat bank and a meadow with some trees (fig. 66). The wall Eltville-Walluf does not continue here. Interviewed employees of the waterworks told me about the total absence of lizards in their area in contrast to the bank at Eltville, and upon my visits to the area I have not seen any.

There are wall lizards in the Eastern top of Schierstein harbour as well as at the harbour entry point on both sides of the Dykerhoff harbour bridge, built in 1967. At the harbour entry the lizards are mainly on the eastern, upstream, Rhine-sided and south-facing dam near the DLRG building (fig. 67) and the decommissioned buildings of the river control unit; they are rare on the western, downstream, Rhine-sided and south-facing dam near the campground. They co-exist with sand lizards, which prefer the parts of the dams which are covered by weedy vegetation (fig. 76). It seems to me that the wall lizards have been transported more or less accidentally to the harbour entry and then spread into the Eastern and South-facing portion of the harbour. The western, larger part of the harbour, is devoid of lizards due to the heavy pedestrian and dog-walker traffic as well as the predation by crows and straying cats.

By morphology and behaviour, the wall lizards at Schierstein harbour (figs. 68-75) are *Podarcis muralis brongniardii*. I think that there is an influence of both, the Eastern France clade and the Western France clade, in this population. The dark males and the "buckskin" type (figs. 73 and 74) as well as the prominent axillary ocellae are signs for the Western France clade. However, the colouration is not as contrasted and distinct as in pure Western France clade

animals, and by their general appearance as well as their behaviour, the influence of the Eastern clade seems to prevail. As Schierstein harbour entry is directly opposite to Kreuzer Hof, an accidental transportation to and fro seems probable in view of the permanent pleasure boat traffic. A rafting or drifting from Mainz harbour is improbable in view of the islands in the Rhine and the direction of the currents. A release of "quarry lizards" at the eastern end of the harbour is quite probable in view of the similarity of the populations, but a dispersal on the Rhine dam along the flood area seems to be quite problematic; there seem to be distribution gaps along the flood line of the river, which is accessible only with difficulty.

#### b) The Cyperus and Hessler populations

Heimes (1990) mentioned a small occurrence south of Wiesbaden that had its origin in released specimens of several European countries, and Schulte (2008) has relied on this. Fuhrmann could not find the animals at Cyperus-Park (2005a), but in the neighbouring Dyckerhoff quarry (2005b). Hessische Gesellschaft für Ornithologie pp. (2015) reported a population of about 200 individuals on a stone wall located in "Acre 29, agricultural land West of Fort Biehler"; this locality was specified by Zitzmann & Malten (2011, 2012) to be a stone wall in Hessler Hof in Mainz-Kastel, though not reflected on their maps. Schulte did not include this location in his more recent listings (e.g. Deichsel & Schulte 2015, Schulte & Deichsel 2015).

The following account relies has been enormously facilitated by the hospitality of Mrs. Hessler of Hessler farm and the President of Cyperus, Mrs. I. Jungels, and its members as well as Mr. K.-H. Schneider of the Schneider plant nursery, who readily told me about the history of their premises, the early release of the lizards and their old and new distribution:

The wall lizard populations are found East of Wiesbaden and East of Highway 673 and the parallel railway tracks (for a sketch map see fig. 77). South of today's main garbage collection point and a light industry area lies a south-facing slope on the Northeastern territory of Mainz-Kastel. The population extends between two tracks running parallel to the highway, viz. "Unterer Zwerchweg" and „Oberer Zwerchweg“.

The Cyperus population as its origin on a south-facing stone wall of a former vineyard which today is overgrown by weeds and partially shaded by trees, which stretches along a track called "Oberer Zwerchweg" (fig. 78). Wall lizards from Southern Europe, evidently mainly from Northern Italy (e.g. Lake Garda), have been released on this wall before, during and after WW I by members of "Cyperus 1901 e.V. - Verein für Aquaristik, Terraristik und Naturschutz", a local association of aquarium, terrarium, and nature lovers. The city of Mainz is now the owner of the core area, which has been leased to Cyperus. Cyperus has water rights and has built small ponds as well as an association house and a terrarium house on the premises. There you find the wall lizards everywhere; while they were widely scattered before 2015, the population has increased since my advice of 2015 has been observed: Some trees have been cut, most bushes have been cleared, and the area has been fenced to keep the stray cats out.

A southwestern portion of the former Cyperus leasehold has been turned over to another lessee, which runs a pet zoo. Because of the rats and the mice, the zoo keeps some cats, and they have eliminated the lizards from the zoo area; you may find lizards only rarely as accidental entries.

East of the Cyperus area, there is the Hessler horse farm; in an unattended meadow, it has a stone wall (fig. 79) which now is the second core area for a dense population of rather large

Italian wall lizards. These Hessler lizards have no black bellies, but have heavily reticulated yellow and green males (figs. 81, 83-85). Either this rather isolated population is based on a separate hybridisation of *Podarcis muralis maculiventris* x *Podarcis muralis nigriventris* (for which I have followed the tradition to name them *Podarcis muralis brueggemanni*, see Börner 2014), or the *nigriventris* influence is waning in the Cyperus population. This latter alternative is in harmony with Mrs. Jungels' statement that in previous years she has seen green wall lizards on the ancient wall along Oberer Zwerchweg and our findings in the Cyperus area as well as the recent photos of definitely yellow specimens (figs. 91, 93, 94, 96-106, 108) and just two greenish lizards from the Cyperus area (figs. 92, 107). For the sake of clarity, the populations will be named here "the Hessler (sub-)population" (*Podarcis muralis maculiventris* x *nigriventris*) and "the Cyperus population" (*Podarcis muralis cf. maculiventris*).

North of Hessler farm there is a garden colony, into which the wall lizards from the Cyperus area have spread, and further to the East there are the Dyckerhoff quarries, into one of which the Cyperus lizards seem to have spread as well, while the other one has been turned into a landfill and still another into a nature preserve.

In earlier times, there was a railway track running from near the quarry to the West, and the wall lizards were reported to have reached via this track a plant nursery and the neighbouring cemetery of Wiesbaden-Erbenheim, which are a little up on a plateau with fields, where the westwind hits more strongly than on the south-facing low part of the slope, where Cyperus and its neighbours are situated. The railway track has been decommissioned in connection with an extension of the US facility Clay Airfield. The track is now covered with bushes and trees and does not have any wall lizards. So the connection to the main area of the wall lizards has been broken. While the track, the plant nursery and maybe the cemetery have had wall lizards, that part of the population is now extinct, obviously due to a lack of creviced vertical structures, on which the Cyperus lizards depend, and the predation by cats and birds of prey. Moreover, the track and the plant nursery still have sand lizards (fig. 110), which are typical for the area and have a competitive advantage due to their much lower activity temperature and their preference for a flat terrain. There are no lizards at all in the tree-shaded cemetery.

To the East, the wall lizards have spread from the Cyperus land into another small garden colony which is also situated on the lower part of the south-facing slope.

The farmland belt around the quarry and the Hessler and Cyperus areas as well as the lower temperatures uphill limit any further contingent expansion of the wall lizards to the North or the East. In the West, I have not found any wall lizard in the busy industrial park or near the rail-tracks. To the South, there is a row of fields without vertical structures, then a highway which is crossed by small bridges and a shaded sink connecting the Dyckerhoff quarry with the lime works and a facility for concrete.

Basically, we can now distinguish two populations, the rather isolated Hessler one, as discussed above, and the more expanded Cyperus one (see fig. 77).

The Cyperus wall lizards are, at least predominantly, *Podarcis muralis maculiventris*, Southern Alps clade, and are referred to as *Podarcis muralis cf. maculiventris*:

Adults are larger (by about 0.5 cm SVL) and heavier than our indigenous ones.

The ground colour on the back is a full brown. In the Cyperus population, lizards with green backs, which are diagnostic for the subspecies *nigriventris* and may also occur in *maculiventris* (Venetian clade) due to hybridisation, are increasingly rare (fig. 92, 107). The green colour seems to be replaced by yellow, and the photos have been arranged to show the transition

from brown and heavily marked to light-coloured males with less conspicuous markings (figs. 95-102).

All lizards show a heavily ocellated pattern (figs. 81-109 and also für Hessler population figs. 80-90). This is evident even in neonates and juveniles, as at least their supraciliary stripe consists of a series of small light spots, and the same is often true for the supralabial stripe (figs. 92, 108-109). This is usually not the case with *Podarcis muralis brongniadii* (Eastern France clade); less than 10 % of its neonates and juveniles show an ocellated supraciliary stripe.

In consequence of the ocellae-pattern, the most males have dark transversal bars in the temporal stripe which are spaced rather widely and are still discernible as ocellae rims (figs. 81, 92, 95-99, 102). Even on the center back of males, the ocellae can be diminished into light spots and their rims may be so broad and confluent as to reduce the ground colour completely, presenting a completely dark animal with light yellow spotting (figs. 81, 96-98 and for Hessler population figs. 83-85).

The females also show an ocellated pattern (figs. 104-107 and for Hessler population figs. 80, 86-88)

The underside is not heavily marked black, as it is diagnostic for *Podarcis muralis nigriventris* of Tuscany. However, some lizards may be a little darker on the underside than our indigenous wall lizards; then the labials and chin have deep black rather than dark stripes, the throat has somewhat larger round spots and the outer ventrals are grey or have dark grey spots. But other lizards of these populations seem to lack such distinctive marks. The underside is usually white, sometimes yellow.

The blue scales of the outer ventrals and the axillary ocellae seem to be more frequent and, if present, more prominent than in the majority of our wall lizards.

The juveniles show a greyish tailtip (figs. 94, 109); neonates usually have a greenish tinge, which is lost after the first week. In contrast, the neonates of the Eastern France clade have a dark grey tailtip which later usually turns brownish, and those of the Western France clade have a greyish tailtip which turns just lighter.

Deichsel & Schulte (2015) add that the vertebral line may be a black band or may consist of broad spots; in the Cyperus and Hessler populations this is not always the case (figs. 93, 104-106 and for the Hessler population figs. 86, 88, 90).

So the main distinction in the field is by (1) the larger size of the adults, (2) the prominent ocellation laterally and dorsally for all age classes, (3) a yellow or green colouration of the back, if present, (4) in neonates a light grey tail-tip with a greenish hue.

The Cyperus and the Hessler lizards have a distinctly higher preference and activity temperature than our indigenous wall lizards. The Cyperus lizards are still shy and fugitive when our lizards are already active and are still out and busy when our lizards retreat from the heat.

The Cyperus and the Hessler lizards are bound to vertical structures and visit the flat areas basically only for hunting or chasing opponents. All social interactions take place on the vertical structure. In flight, the lizards always move upwards. It is a noteworthy experience to see 5-7 animals simultaneously running up a 2.5 m high wall even when coming out of the vegetation at the bottom of the wall.

These special heat and habitat requirements also differ from those of the indigenous sand lizard. In the Cyperus area, the sand lizard is rare due to its preference for vegetated and

cooler areas. On the plateau, e.g. in the plant nursery, neither the allochthonous nor the autochthonous clades of wall lizards could establish a resilient colony and were outcompeted by the sand lizard, which is now common again.

Finally, the recent development of a prevalence of yellow-backed instead of green-backed lizards in the Cyperus area in comparison to the Hessler area should be considered beyond the status report.

One hypothesis is that the green-backed animals have been released only in the Hessler area so that only very few of their kind made it into the old stone wall of the Cyperus area and their genes were too few to persist on the long run, which is a simple numbers play. However, this is in conflict with the observation, that from the beginning of the last century until about 2005, green lizards were in the Cyperus area, lately most concentrated on the old stone wall, and have diminished on the wall since 2005 with an increasing vegetation.

The other, historically more probable hypothesis is that some green-backed lizards have been released by the Cyperus members on or near the old stone wall near the Cyperus headquarters and have made it to the Hessler wall. There they found a hot vertical site for a quick warming and have been able to maintain the green colour. With the strong eutrophy of the Cyperus area and at the old stone wall, shading hindered a quick warm-up and reduced the heat in weedy patches; this necessitated longer stays in the sunny patches, where the substrate (stone, wood or barren earth) is brown and for the benefit of predators green-backed lizards stand out much more than yellow-backed ones. Since 2005, the old stone wall has been cleared of vegetation about every other year, but the green-backed lizards have not rebounded; this is another sign for their previous extinction as well as for a greater fitness of the yellow-backed lizards.

This second hypothesis is conform with the hypothesis that the green-backed wall lizards (ssp. *nigriventris*) have evolved in Tuscany because there (1) the general temperature is higher and the period of exposed warming-up is shorter and (2) the temperature in the weed layer, where the lizards hunt and interact and spend a lot of time and need camouflage, is higher, than in Northern Italy and the Abruzzes mountains, where the brown-backed type is found.

#### c) Amoeneburg station

Fuhrmann (2005a) did not find wall lizards at the Amoeneburg railway station, which is close to the Cyperus area. Although I have failed to find lizards near the bridges over the highway 673, which separates the railway tracks from the Cyperus area, lizards have been obvious in the railway area south of Amoeneburg station since 2016 (figs. 111). In most respects, they are typical Cyperus lizards, viz. *Podarcis muralis* cf. *maculiventris*. Most lizards have an ocellated pattern on light or yellowish brown, a broader vertebral line, and a white underside (figs. 112, 115-122). One male shows *nigriventris* traits as e.g. a dark pattern with yellow spots and a dark underside (fig. 113). The neonates start to show the variation in colour and pattern and a light grey or yellowish tail (figs. 120-122).

#### d) Mainz-Kastel

The south tip of Mainz-Kastel near Theodor-Heuss Bridge, on which a throughway crosses the Rhine for Mainz central city, has wall lizards on the Rhine embankment and at the railway tracks near Rampenstraße, which is close to the embankment. Wall lizards are also found a few hundred meters further southeast near the Mainz-Kastel railway station.

The lizards near the railway tracks and at the railway station (figs. 123-126 and 132-135, respectively) are quite similar. Superficially they look like *Cyperus* lizards (especially fig. 123, 128, 129b with a greenish hue), and the land connection is by rail to Amoenburg and the Dyckerhoff quarries, though the use of this route has been neither tested nor proven. Moreover, their full brown basic colouration, the thin vertebral line, and the plain underside are in line with the Western France clade from the opposite side of the Rhine. Even without a genetic assessment, it is probable that these lizards have to be seen in connection with the relocation efforts for the Ilmenau animals, being released either on the rail tracks or on the embankment. In consequence, their subspecies and clade affiliation have to remain open for the time being, although I feel that the traits of *Podarcis muralis brongniardii*, Western France clade prevail.

The situation on the Rhine embankment is a little bit more complex:

This embankment (fig. 127) runs from Theodor-Heuss-Bridge about 1 km to the Northeast, where a wooded area starts to run along the river. The embankment consists of two stone slopes, a lower slope bordering the water and carrying bushes and trees and a higher slope basically with only very few weeds. The lizards occupy the sunny patches of the lower slope above the usual flood line.

Subject to genetic examination, I think that these brown wall lizards are intermediates between the indigenous line (*Podarcis muralis brongniardii*, Eastern France clade) and the Ilmenau lizards (*Podarcis muralis brongniardii*, Western France clade). There is evidence from morphology and behaviour.

Several traits indicate the Western France clade: Many animals are spotted (figs. 128, 131-132) or ocellated (figs. 133, 135). Most have at least one distinct axillary ocella. They are light underneath. One juvenile is of the buckskin type (fig. 134). The bigger adults do not emerge from their crevices until air temperatures are above ca. 25° C.

Some animals look and behave like those of the Eastern France clade (fig. 128-130). They seem to be fewer and, although spread throughout the range, they are mainly encountered in the western, more shaded part of the embankment.

The closer the embankments come to the railway tracks, the more the Western France line is dominant (see figs. 123, 128, 132-133, 135); the further away the embankments are from the railway tracks, the more our indigenous line is seen (see figs. 129b, 130). This has been most conspicuous in the many neonates and juveniles which swarm the embankment in mid-August.

#### e) Mainz- Kostheim

The railway track running from Mainz-Kastel to the East, the local cemetery and the Rhine and Main embankments lack wall lizards. The Rhine dam carries a dense bushy vegetation with few interruptions and consists of tightly packed stones, often plastered with concrete, which lack holes and crevices (fig. 136). Along the Main there are flat banks shaded by trees; these banks are prone to flooding (fig. 137).

#### 5. The Wiesbaden area

Fuhrmann (2005a) did not find wall lizards at some other reported localities: Wiesbaden railway station Biebrich, in the vineyard Neuberg of Mainz-Kostheim and in the quarry near "Taunusblick" at Delkenheim. My research has shown:

The lizards from south of Amoenburg station may be present at that station and may have spreaded to Biebrich station. Biebrich's bank on the Rhine is dotted with industrial plants and has no lizards.

The vineyard "Neuberg" is a gentle slope without vertical structures. There is not even a hint for the existence of wall lizards; no neighbour or farmer has ever seen any, not even faeces have been found, and I had no unknown escapes of small animals.

The other vineyards between Mainz-Kostheim and Hochheim are devoid of wall lizards, too; there are only a few stone walls, and they lack holes and crevices because of new concrete plastering.

At Delkenheim there is one gravel quarry which has been transformed into a golf course. It has no wall lizards. There is no locality "Taunusblick" in or near Delkenheim. A locality with this name is in the Taunus hills near Niedernhausen, where there are only viviparous lizards.

All reports of wall lizards in the cemeteries of Wiesbaden and in the Wiesbaden area in general have been checked. Unless indicated otherwise in this report, they are all based on juvenile sand lizards. Sand lizards are not unusual in the area and are found in garden colonies, which are usually adjacent to the cemeteries, as well as in orchards, pastures, cemeteries, railway stations, on railway tracks and highway embankments etc. I have got the impression that nearly all locals call any brown lizard seen on a stone, a "wall lizard".

Looking east of Wiesbaden, the next wall lizard populations is said to be in the protected fully fenced area of the Flörsheim-Weilheim quarry; in the publicly accessible area, I have not been able to confirm this report.

There are reliable reports of wall lizards on the tracks of the old Frankfurt harbour railway (Zitzmann & Malten 2012, title photo) and in the nature park in Frankfurt-Europaviertel, to where the population of the railway freight terminal (Seipp et al. 1998) has been relocated (Dietermann 2018). This latter population has been examined genetically; it belongs to the indigenous line *Podarcis muralis brongniardii*, Eastern France clade (Schulte 2008), and this can also be seen on a photo (male depicted by Dietermann 2018; the lizard depicted by Harting 2011 cannot be identified beyond the species level)..

## Summary

In view of the import of allochthonous clades of the Common Wall Lizard *Podarcis muralis* into Germany, the Mainz Basin presents an interesting situation.

Rhineland-Palatinate and Hessen have the indigenous subspecies *brongniardii*, Eastern France clade. It is restricted to the hill areas. On the south bank of the Rhine in the Mainz Basin it has its southernmost locality at Bingen-Gaulsheim. On the north bank its distribution in the Mainz Basin becomes spottier towards the East, because the south-facing slopes of the Rheingau get less and less steep; along the Rhine the contingent distribution area ends near Oestrich-Winkel.

Some 30 km east of Gaulsheim, the Mainz-Budenheim quarry and its vicinity harbour the subspecies *brongniardii*, Western France clade. This is due to a relocation in 2007-2009 from the "Ilmenauer Aue", a railway track habitat in central Mainz along the lower Gonsbach creek. The Ilmenauer Aue and the adjacent industrial park near the freight harbour have been under substantial construction, but some lizards can still be found in the area. The wall lizards of the south embankment of the harbour peninsula near the harbour entry have a yellow brown basic

dorsal colouration, which may have given rise to the buckskin type of colouration and pattern which may be observed in the Budenheim quarry. East of the quarry and its vicinity, the lizards are found at Budenheim in the gardens of Kreuzer Hof, a small settlement on the Rhine.

As some lizards of the relocation effort may not have arrived in the quarry, they may have been released in supposedly suitable habitats. This rather than rafting with the Rhine currents may explain their suspected mixing with the indigenous clade on the opposite, northern bank of the Rhine in two locations:

- the wall along the towing path between Eltville and Walluf (east of Oestrich-Winkel), where they form a large population, which is basically tied to the wall, and has expanded neither into the city of Eltville nor into the Rheingau hills of the hinterland nor into the eastern part of Walluf;
- the Rhine embankment of Mainz-Kastel (near Theodor-Heuss bridge), where they drive the Eastern France clade into the shadier areas, particularly those on the edge of the distribution area; the Western France clade has spread to the nearby railway tracks, southeast at least to Mainz-Kastel railway station.. .

While the protected meadowlands of the Schierstein water works on the Rhine east of Walluf are without lizards, a small population of wall lizards exists at Schierstein harbour entry and the eastern end of the harbour. Predominantly these lizards show the characters of the indigenous Eastern France clade, but sporadic Western France clade influence cannot be excluded.

In the southeast of Wiesbaden, in the lower portion of a south-facing slope of a former, now long abandoned vineyard, there is the *Cyperus* population of wall lizards. It stems from imports mainly from Northern Italy before, during and shortly after WW I. It is said to have extended to the Dyckerhoff quarries in the northwest, to the Erbenheim cemetery and its vicinity in the north where it is now extinct due to the harsher uphill climate and a lack of unshaded vertical structures, and to the allotment gardens in the east while elsewhere being surrounded by impenetrable fields and woods. This population is dominated by the subspecies *maculiventris*, Southern Alps clade. In the main population the green dorsum, which characteristic of the subspecies *nigriventris*, has been reduced to yellow spots; this is explained by the eutrophy in the main new habitat. However, the green colour still exists in some rare individuals and especially in the Hessler farm subpopulation

Most other locality reports for wall lizards at least in the Wiesbaden area are erroneous; they are based on juvenile sand lizards; the sand lizard *Lacerta a. agilis* is common in the Mainz Basin.

The morphology and behaviour of the three main wall lizard clades in the Mainz basin (ssp. *brongniadii*, Eastern France clade and Western France clade, as well as ssp. *maculiventris*) are compared in order to facilitate recognition in the field and to substantiate the lack of substantial threat for the indigenous lizard fauna. The special temperature and habitat requirements as well as the lack of inherited specific threat avoidance techniques (beyond avoiding the flood-prone areas) of the southern clades of the Common Wall Lizard restrict them to a spotty distribution in Germany.

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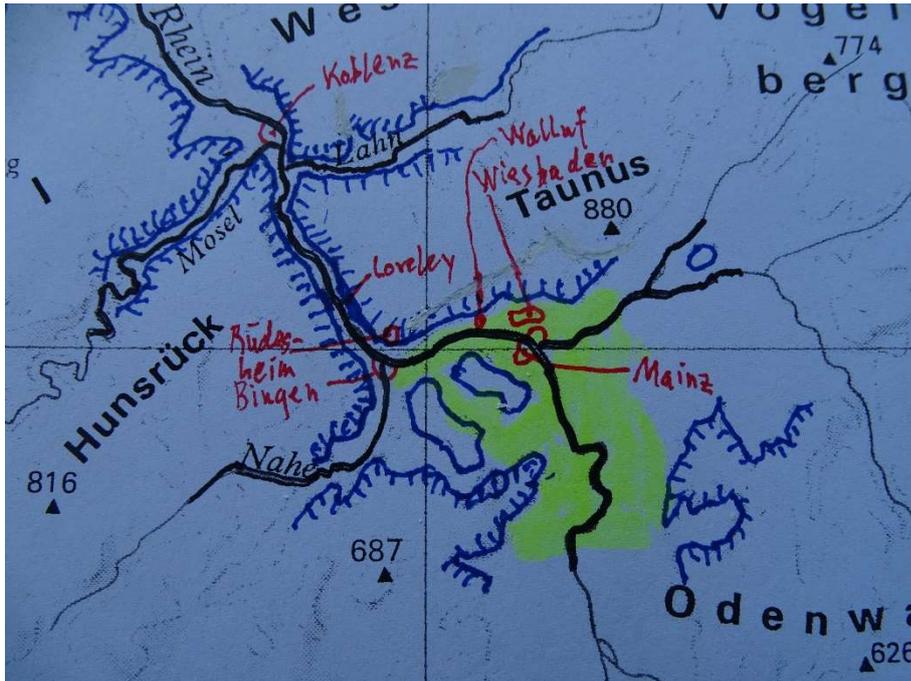


Fig. 1 Sketch of the Upper Middle Rhine with the Mainz Basin, based on Trautmann Atlas-Edition, Neuer Grosser Weltatlas, Munich (Compact) 2001, p. 8  
black = river, blue = 200m contour line, red = cities, yellow = Mainz Basin

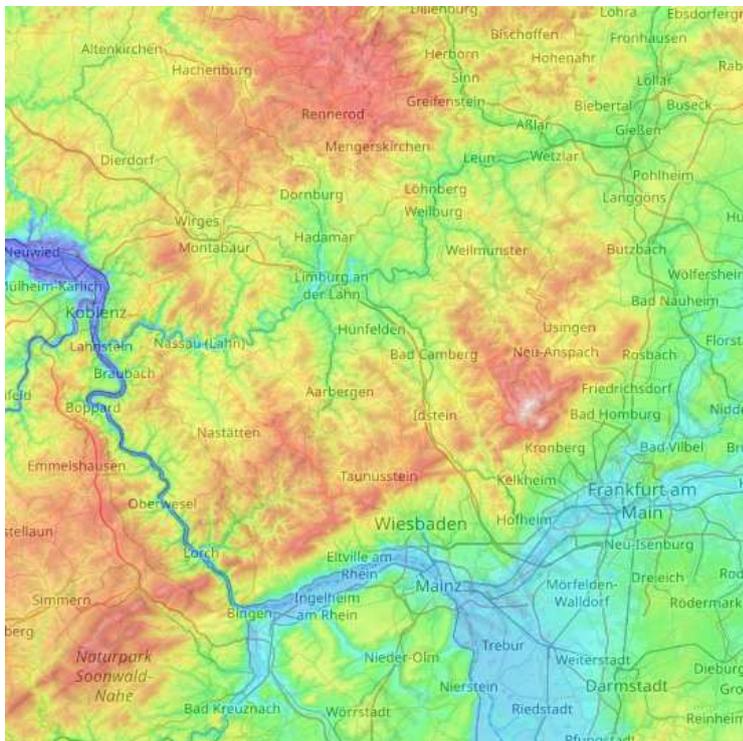


Fig. 2 Sketch of the Mainz Basin, map available at: <https://de-de.topographic-map.com/maps/zkxd/Taunus/>  
The blue halfmoon in the lower half is a low flat area which corresponds to the Mainz Basin.



Fig. 3 *Podarcis muralis brongniardii*, Eastern France clade, male at Kamp-Bornhofen, 30.03.2019



Fig. 4 *Podarcis muralis brongniardii*, Eastern France clade, male at Kamp-Bornhofen, 30.03.2019



Fig. 5 *Podarcis muralis brongniardii*, Eastern France clade, male at Eagle Rock near Kördorf, 12.08.2014



Fig. 6 *Podarcis muralis brongniardii*, Eastern France clade, male at Schloss Johannisberg, 06.06.2014



Fig. 7 *Podarcis muralis brongniardii*, Eastern France clade, male at Rhenser Mühlthal, 03.07.2018



Fig. 8 *Podarcis muralis brongniardii*, Eastern France clade, male at Ahl, Friedrichsegen, 12.07.2020



Fig. 9 *Podarcis muralis brongniardii*, Eastern France clade, female near Braubach, 12.08.2018



Fig. 10 *Podarcis muralis brongniardii*, Eastern France clade, on Ahl, Friedrichsegen, 25.07.2018



Fig. 11 *Podarcis muralis brongniardii*, Eastern France clade, female on Mouse castle above St. Goarshausen, 14.08.2017



Fig. 12 *Podarcis muralis brongniardii*, Eastern France clade, juvenile on Mouse Castle above St. Goarshausen, 14.08.2017



Fig. 13 *Podarcis muralis brongniardii*, Eastern France clade, and *Lacerta a. agilis*, neonates on nesting hill near Braubach, 06.09.2018



Fig. 14 *Podarcis muralis brongniardii*, Eastern France clade, male on tree above Filsen, 12.05.2018

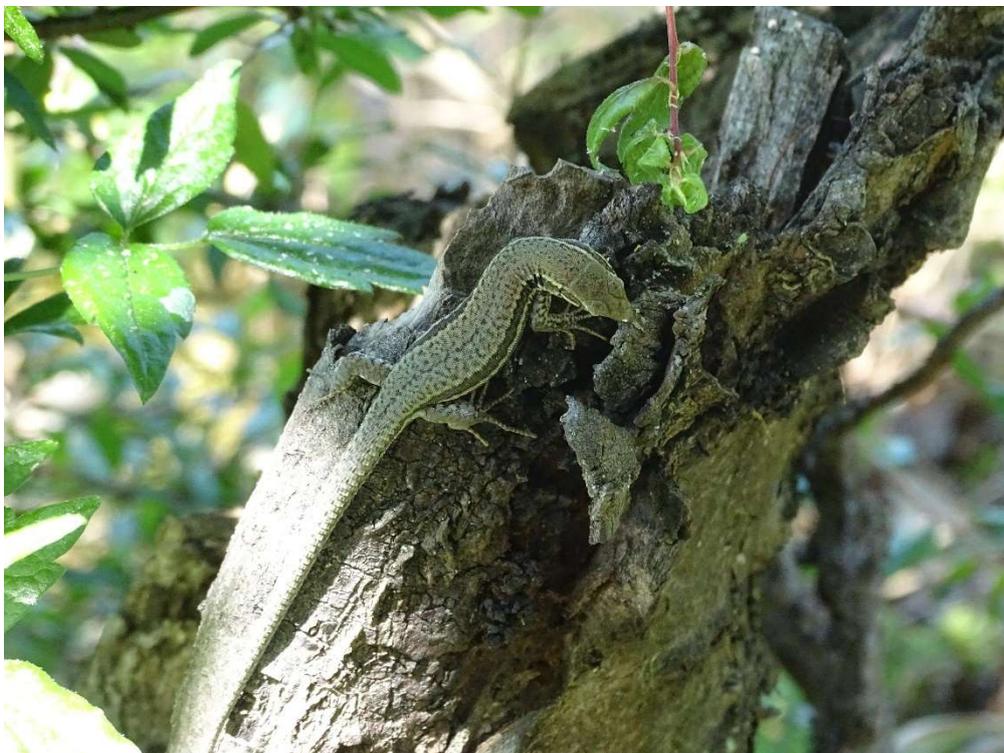


Fig. 15 *Podarcis muralis brongniardii*, Eastern France clade, female on ta tree near St. Goarshausen, 07.05.2020



Fig. 18 *Podarcis muralis brongniardii*, Eastern clade, female, northeast of Bingen-Gaulsheim, 22.08.2020

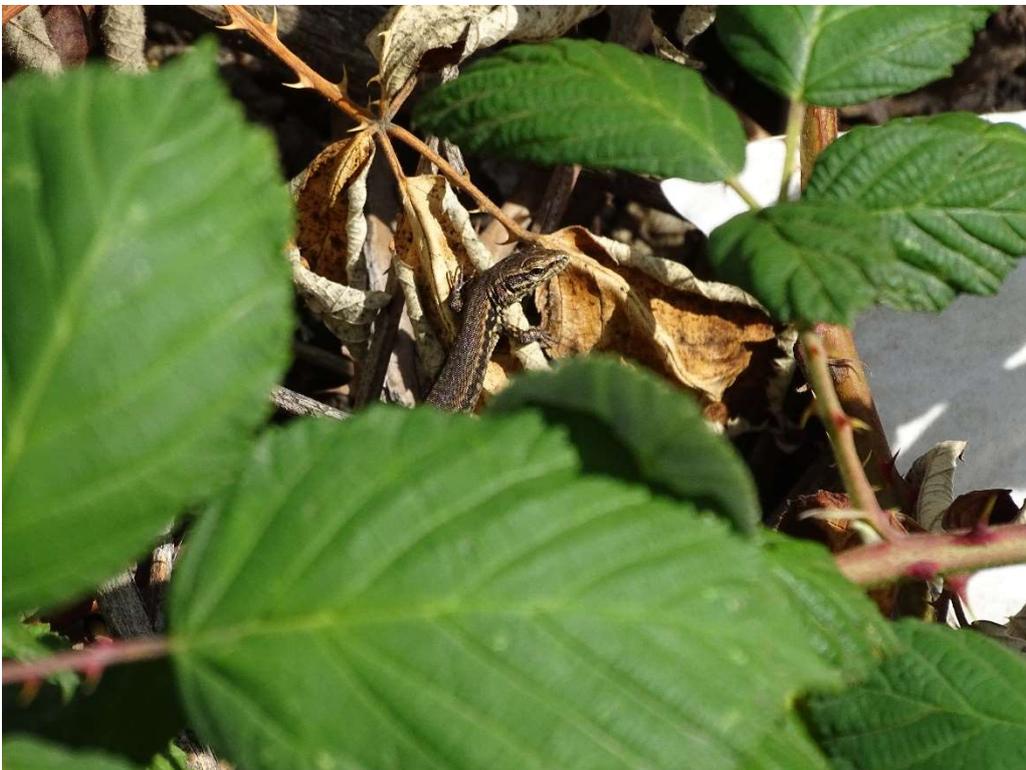


Fig. 19 *Podarcis muralis brongniardii*, Eastern clade, juvenile, north of Bingen - Gaulsheim, 22.08.2020



Fig. 20 Railway track from Bingen to Ingelheim, near Bingen-Gaulsheim station, 22.08.2020



Fig. 21 *Podarcis muralis brongniardii*, Western France clade, male, Mainz-Budenheim quarry, 17.08.2020



Fig. 22 *Podarcis muralis brongniardii*, Western France clade, male, northwest rim of Mainz-Budenheim quarry, 17.08.2020



Fig. 23 *Podarcis muralis brongniardii*, Western France clade, male, northwest rim of Mainz-Budenheim quarry, 17.08.2020



Fig. 24 *Podarcis muralis brongniardii*, Western France clade, female, Mainz-Budenheim quarry, 17.08.2020



Fig. 25 *Podarcis muralis brongniardii*, Western France clade, female, northwest rim of Mainz-Budenheim quarry, 17.08.2020



Fig. 26 *Podarcis muralis brongniardii*, Western France clade, buckskin female, Mainz-Budenheim quarry, 17.08.2020



Fig. 27 *Podarcis muralis brongniardii*, Western France clade, buckskin female, northwest rim of Mainz-Budenheim quarry, 17.08.2020



Fig. 28 *Podarcis muralis brongniardii*, Western France clade, buckskin female, northwest rim of Mainz-Budenheim quarry, 17.08.2020



Fig. 29 *Podarcis muralis brongniardii*, Western France clade, juvenile, Mainz-Budenheim quarry, 17.08.2020



Fig. 30 *Podarcis muralis brongniardii*, Western France clade, buckskin juvenile, Mainz-Budenheim quarry, 17.08.2020



Fig. 31 *Podarcis muralis brongniardii*, Western France clade, male, Kreuzer Hof, 29.08.2020



Fig. 32 *Podarcis muralis brongniardii*, Western France clade, female, Kreuzer Hof, 29.08.2020



Fig. 33 *Podarcis muralis brongniardii*, Western France clade, female, Kreuzer Hof, 29.08.2020



Fig. 34 Mainz freight harbour, look inward to the east, 28.08.2020



Fig. 35 Mainz freight harbour, looking outward to the west, 29.08.2020



Fig. 36 *Podarcis muralis brongniardii*, Western France clade, male at Mainz freight harbour, 28.08.2020



Fig. 37 *Podarcis muralis brongniardii*, Western France clade, male at Mainz freight harbour, 28.08.2020



Fig. 38 *Podarcis muralis brongniardii*, Western France clade, male at Mainz freight harbour, 28.08.2020



Fig. 39 *Podarcis muralis brongniardii*, Western France clade, female at Mainz freight harbour, 28.08.2020



Fig. 40 *Podarcis muralis brongniardii*, Western France clade, female at Mainz freight harbour, 28.08.2020



Fig. 41 *Podarcis muralis brongniardii*, Western France clade, yearling at Mainz freight harbour, 28.08.2020



Fig.42 *Podarcis muralis*, male at station Mainz-Nord, 28.08.2020



Fig. 43 *Podarcis muralis*, male at station Mainz-Nord, 28.08.2020



Fig. 44 *Podarcis muralis*, female at station Mainz-Nord, 28.08.2020



Fig. 45 *Podarcis muralis*, female at station Mainz-Nord, 28.08.2020



Fig. 46 *Podarcis muralis*, neonate at station Mainz-Nord, 28.08.2020



Fig. 47 *Podarcis muralis*, neonate at station Mainz-Nord, 28.08.2020



Fig. 48 Rheingau, from Johannisberg castle, 06.06.2014



Fig. 49 Railway track near Hattenheim, Rheingau, 12.03.2015



Fig. 50 *Podarcis muralis brongniardii*, Eastern France clade, female on the railtrack near Hattenheim, 12.03.2015



Fig. 51 Towing path from Eltville to Walluf, 21.08.2020



Fig. 52 *Podarcis muralis brongniardii*, Eltville-Walluf population, male on the wall of the towing path near Eltville, 21.08.2020



Fig. 53 *Podarcis muralis brongniardii*, Eltville-Walluf population, male on the wall of the towing path near Eltville, 21.08.2020



Fig. 54 *Podarcis muralis brongniardii*, Eltville-Walluf population, male on the wall of the towing path in Walluf, 21.08.2020



Fig.55 *Podarcis muralis brongniardii*, Eltville-Walluf population, male on the wall of the towing path in Walluf, 21.08.2020



Fig. 56 *Podarcis muralis brongniardii*, Eltville-Walluf population, male on the wall of the towing path near Eltville, 21.08.2020



Fig. 57 *Podarcis muralis brongniardii*, Eltville-Walluf population, young female on the wall of the towing path near Eltville, 21.08.2020



Fig. 58 *Podarcis muralis brongniardii*, Eltville-Walluf population, female on the wall of the towing path near Eltville, 21.08.2020



Fig. 59 *Podarcis muralis brongniardii*, Eltville-Walluf population, female on the wall of the towing path in Walluf, 21.08.2020



Fig. 60 *Podarcis muralis brongniardii*, Eltville-Walluf population, female on the wall of the towing path near Eltville, 21.08.2020



Fig. 61 *Podarcis muralis brongniardii*, Eltville-Walluf population, juvenile on the wall the towing path near Eltville, 21.08.2020



Fig. 62 *Podarcis muralis brongniardii*, Eltville-Walluf population, juvenile on the wall the towing path near Eltville, 21.08.2020



Fig. 63 *Podarcis muralis brongniardii*, Eltville-Walluf population, juvenile on the wall the towing path near Eltville, 21.08.2020



Fig. 64 *Podarcis muralis brongniardii*, Eltville-Walluf population, juvenile male on the wall the towing path near Eltville, 21.08.2020



Fig. 65 *Podarcis muralis brongniardii*, Eltville-Walluf population, juvenile on the wall the towing path in Walluf, 21.08.2020



Fig. 66 Schierstein waterworks and protected area, photo by Hessen Wasser GmbH on a public information board



Fig. 67 Schierstein harbour entry, 21.08.2020



Fig. 68 *Podarcis muralis brongniardii*, Schierstein population, male, East dam of Schierstein harbour entry, 21.08.2020



Fig. 69 *Podarcis muralis brongniardii*, Schierstein population, male at eastern end of Schierstein harbour, 21.08.2020



Fig. 70 *Podarcis muralis brongniardii*, Schierstein population, male at the eastern end of Schierstein harbour, 21.08.2020



Fig. 71 *Podarcis muralis brongniardii*, Schierstein population, female on the eastern dam of Schierstein harbour entry, 21.08.2020



Fig. 72 *Podarcis muralis brongniardii*, Schierstein population, female on the eastern dam of Schierstein harbour entry, 21.08.2020



Fig. 73 *Podarcis muralis brongniardii*, Schierstein population, female on the eastern dam of Schierstein harbour entry, 21.08.2020



Fig. 74 *Podarcis muralis brongniardii*, Schierstein population, female on the eastern dam of Schierstein harbour entry, 21.08.2020



Fig. 75 *Podarcis muralis brongniardii*, Schierstein population, juvenile on the western dam of Schierstein harbour entry, 21.08.2020



Fig. 76 *Lacerta a. agilis*, juvenile on the western dam of the Schierstein harbour entry, 21.08.2020

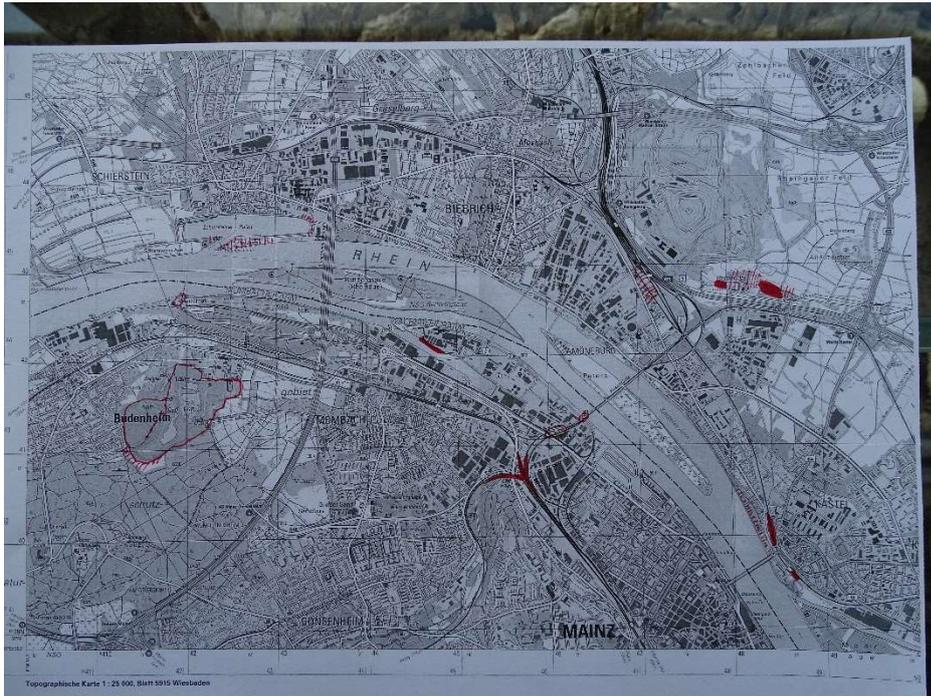


Fig. 77 Map of the Mainz-Wiesbaden area, based on:  
Hessisches Landesamt für Bodenmanagement und Geoinformation,  
Topographische Karte 5915 Wiesbaden, 1:25.000, 1 square = 1 kilometer square  
red = wall lizard core area, red stripes = wall lizard range



Fig. 78 The stone wall at Oberer Zwerchweg, Cyperus area, 15.08.2020



Fig. 79 The stone wall and building at Hessler farm, 02.06.2017



Fig. 80 *Podarcis muralis maculiventris x nigriventris*, Hessler population, female, Hessler farm, 02.06.2017



Fig. 81 *Podarcis muralis maculiventris x nigriventris*, Hessler population, male, Hessler farm, 02.06.2017



Fig. 82 *Podarcis muralis maculiventris x nigriventris*, Hessler population, male, Hessler farm, 02.06.2017



Fig. 83 *Podarcis muralis maculiventris x nigriventris*, Hessler population, male, Hessler farm, 02.06.2017



Fig. 84 *Podarcis muralis maculiventris x nigriventris*, Hessler population, male, Hessler farm, 02.06.2017. same as fig. 93



Fig. 85 *Podarcis muralis maculiventris x nigriventris*, Hessler population, pair, Hessler farm, 02.06.2017



Fig. 86 *Podarcis muralis maculiventris x nigriventris*, Hessler population, female, Hessler farm, 02.06.2017



Fig. 87 *Podarcis muralis maculiventris x nigriventris*, Hessler population, female, Hessler farm, 02.06.2017



Fig. 88 *Podarcis muralis maculiventris x nigriventris*, Hessler population, female, Hessler farm, 02.06.2017



Fig. 89 *Podarcis muralis maculiventris x nigriventris*, Hessler population, female, Hessler farm, 02.06.2017



Fig. 90 *Podarcis muralis maculiventris x nigriventris*, Hessler population, female, Hessler farm, 09.07.2017



Fig. 91 *Podarcis muralis* cf. *maculiventris*, Cyperus population, male Cyperus garden, 09.07.2017



Fig. 92 *Podarcis muralis* cf. *maculiventris*, Cyperus population, female Cyperus garden, 09.07.2017



Fig. 93 *Podarcis muralis* cf. *maculiventris*, Cyperus population, female in Cyperus garden, 09.07.2017



Fig. 94 *Podarcis muralis* cf. *maculiventris*, Cyperus population, juvenile in Cyperus garden, Juli 2017, photo by C. Tannenber



Fig. 95 *Podarcis muralis* cf. *maculiventris*, Cyperus population, male, old stone wall, 06.08.2020



Fig. 96 *Podarcis muralis* cf. *maculiventris*, Cyperus population, male in Cyperus garden, 06.08.2020



Fig. 97 *Podarcis muralis* cf. *maculiventris*, Cyperus population, male in Cyperus garden, 06.08.2020



Fig. 98 *Podarcis muralis* cf. *maculiventris*, Cyperus population, male in Cyperus garden, 06.08.2020



Fig. 99 *Podarcis muralis* cf. *maculiventris*, Cyperus population, male in Cyperus garden, 06.08.2020



Fig. 100 *Podarcis muralis* cf. *maculiventris*, Cyperus population, young male in Cyperus garden, 06.08.2020



Fig. 101 *Podarcis muralis cf. maculiventris*, Cyperus population, male, old stone wall, 06.08.2020



Fig. 102 *Podarcis muralis cf. maculiventris*, Cyperus population, male, old stone wall, 15.08.2020



Fig. 103 *Podarcis muralis cf. maculiventris*, Cyperus population, male in Cyperus garden, 06.08.2020



Fig. 104 *Podarcis muralis cf. maculiventris*, Cyperus population, pair, old stone wall, 06.08.2020



Fig. 105 *Podarcis muralis cf. maculiventris*, Cyperus population, female in Cyperus garden, 06.08.2020



Fig. 106 *Podarcis muralis cf. maculiventris*, Cyperus population, female on old stone wall, 06.08.2020



Fig. 107 *Podarcis muralis* cf. *maculiventris*, Cyperus population, female in Cyperus garden, 06.08.2020



Fig. 108 *Podarcis muralis* cf. *maculiventris*, Cyperus population, one year old juvenile on old stone wall, 06.08.2020



Fig. 109 *Podarcis muralis cf. maculiventris*, Cyperus population, juvenile, old stone wall, 06.08.2020



Fig. 110 *Lacerta a. agilis* in the Erbenheim plant nursery, 15.08.2020



Fig. 111 The habitat south of Amoeneburg railway station, 28.08.2020



Fig. 112 *Podarcis muralis maculiventris*, male, south of Amoeneburg station, 28.08.2020



Fig. 113 *Podarcis muralis maculiventris x nigriventris*, male, south of Amoeneburg station, 28.08.2020; this male has a black throat.



Fig. 114 *Podarcis muralis cf. maculiventris*, male, south of Amoeneburg station, 28.08.2020



Fig. 115 *Podarcis muralis cf. maculiventris*, male, south of Amoeneburg station, 28.08.2020



Fig. 116 *Podarcis muralis cf. maculiventris*, female, south of Amoeneburg station, 28.08.2020



Fig. 117 *Podarcis muralis* cf. *maculiventris*, female, south of Amoeneburg station, 28.08.2020



Fig. 118 *Podarcis muralis* cf. *maculiventris*, female, south of Amoeneburg station, 28.08.2020



Fig. 119 *Podarcis muralis* cf. *maculiventris*, female, south of Amoeneburg station, 28.08.2020



Fig. 120 *Podarcis muralis* cf. *maculiventris*, neonate, south of Amoeneburg station, 28.08.2020



Fig. 121 *Podarcis muralis* cf. *maculiventris*, neonate, south of Amoeneburg station, 28.08.2020



Fig. 122 *Podarcis muralis* cf. *maculiventris*, neonate, south of Amoeneburg station, 28.08.2020



Fig. 123 *Podarcis muralis ssp.*, Mainz-Kastel population, male northeast of the main Kastel railway station, 22.08.2020



Fig. 124 *Podarcis muralis ssp.*, Mainz-Kastel population, young male, northeast of the main Kastel railway station, 22.08.2020



Fig. 125 *Podarcis muralis ssp.*, Mainz-Kastel population, female, northeast of the main Kastel railway station, 22.08.2020



Fig. 126 *Podarcis muralis ssp.*, Mainz-Kastel population, female, northeast of the main Kastel railway station, 22.08.2020



Fig. 127 Mainz-Kastel Rhine embankment, the lizards are in the lower slope, 22.08.2020



Fig. 128 *Podarcis muralis* ssp., Mainz-Kastel population, male on the Rhine embankment, 22.08.2020



Fig. 129a *Podarcis muralis ssp.*, Mainz-Kastel population, female on the Rhine embankment, 22.08.2020



Fig. 129b *Podarcis muralis ssp.*, Mainz-Kastel population, female on the Rhine embankment, 22.08.2020



Fig. 130 *Podarcis muralis ssp.*, Mainz-Kastel population, neonate on the Rhine embankment, 22.08.2020



Fig. 131 *Podarcis muralis ssp.*, Mainz-Kastel population, neonate on the Rhine embankment, 22.08.2020



Fig. 132 *Podarcis muralis ssp.*, Mainz-Kastel population, male at the main Kastel railway station, 22.08.2020



Fig. 133 *Podarcis muralis ssp.*, Mainz-Kastel population, female at the main Kastel railway station, 22.08.2020



Fig. 134 *Podarcis muralis* ssp., Mainz-Kastel population, neonate at the main Kastel railway station, 22.08.2020



Fig. 135 *Podarcis muralis* ssp., Mainz-Kastel population, neonate at the amin Kastel railway station, 22.08.2020



Fig. 136 Rhine embankment at Mainz-Kostheim, without lizards, 22.08.2020



Fig. 137 Main embankment at Mainz-Kostheim, without lizards, 22.08.2020

## Saurologica

- No. 1 Revision der Geckonidengattung *Phelsuma* GRAY 1825,  
Köln/ Cologne 20. VIII.1972, 145 pp., figs.
- No. 2 Second contribution to the systematics of the southwest  
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Materials from the Indian subcontinent,  
Köln / Cologne 10.V.1975, 15 pp., 10 tabs, 1. figs., 3 pls.
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- No. 6 Herbstbesuch 2019 bei den Lacerten auf Burg Hardenberg  
bei Göttingen  
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