Summary

In spite of extant diversity, squamates may have lost the phylogenetic signal from the evolutionary events that took place 200 million years ago. Only the fossil record may help to solve controversies around their phylogeny. It is still incomplete but improves with every next year. The skeleton of Triassic lepidosaur *Megachirella wachtleri* (Renesto & Posenato 2003), omitted in earlier studies but examined by myself, may be of a crucial value. It is Middle Triassic in age, and seems morphologically close to the common ancestor of rhynchocephalians and squamates or perhaps is among the earliest squamates (Renesto & Bernardi 2014). Despite its crucial phylogenetic position, it was not taken into account in publications discussing the lepidosaur origins (i.e. Evans & Jones 2010; Jones *et al.* 2013). All this, together with a new material from Poland (Evans & Borsuk-Bialynicka 2009) enables testing hypotheses about the origin and early diversification of the lepidosaur reptiles (Chapter 1). I will demonstrate there that some previously known early lepidosauromorphs already represented the crown lepidosaurs. *Paliguana*, *Megachirella* and *Marmoretta* probably correspond to successive stages of the lizard stem lineage and *Sophineta* may be close to the ancestry of rhynchocephalians, both lineages may have originated already in the Permian. This also means, in phylogenetic terms, that the pleurodont lepidosaurs are paraphyletic to the Rhynchocephalia (Whiteside, 1986).

Another area of uncertainty that requires discussion from paleontological point of view is the time, space and character of the split of the crown Squamata into their main groups (the Dibamidae, Gekkota, Scincioidea, Lacertoidea, Iguania, Serpentes and Anguimorpha). The most apparent disparity between the morphological and molecular data concerns the question, which lineage is the basalmost (Iguania versus Dibamidae). Morphology agrees with molecules that Gekkota is the second basalmost group of squamates. This is congruent with their fossil record reaching probably the Jurassic (Gauthier *et al.* 2012; Daza *et al.* 2014). The next should be Scincioidea and Lacertoidea, either (1) forming a clade according to morphological data (Conrad 2008; Gauthier *et al.* 2012) or (2) splitting separately from the stem, as suggested by molecular studies (Townsend *et al.* 2004; Vidal & Hedges 2005). Some paleontological evidence (Estes 1983; Evans *et al.* 2012; Gauthier *et al.* 2012) suggests that the Jurassic and Cretaceous Paramacellodidae (lizards covered by rectangular osteoderms) are stem-scincoids, while the oldest lacertoids and crown scincoids come from the Cretaceous (Evans *et al.* 2012; Gauthier *et al.* 2012). This is in contrast with two more advanced lineages:
Anguimorpha and Serpentes, the fossil record of which extends back to the Middle Jurassic (Evans & Chure 1999; Evans 2003; Caldwell et al. 2015). I will describe and discuss previously unknown aspects of the anatomy of the Late Jurassic lizard *Ardeosaurus brevipes* (Chapter 2). I have found there traits typical for the Scincidae. This clarifies the time and geographic location of the early diversification of the crown-Scincoida.

Loss of the limbs is one of the most recognizable and frequent processes in the squamate evolution (Greer 1991; Caldwell 2003). Morphological data consistently gather most of the snake-like, limbless taxa together (Estes et al. 1988; Lee 1998; Kearney 2003b; Conrad 2008; Gauthier et al. 2012). Such “clade” usually consist of the amphisbaenians, dibamids, and snakes and is placed close to such groups with tendency to limb reduction as the scincoids, gekkotans, and anguimorphs (Kearney 2003b; Conrad 2008; Gauthier et al. 2012). In some interpretations snakes fell out this group to be allied with mosasaurs (Lee 1998). Molecular studies challenged so close relationships of limbless taxa and put them in completely different places of the Squamata tree (Townsend et al. 2004; Vidal & Hedges 2005; 2009; Wiens et al. 2012). They place the Dibamidae as the basalmost or second basalmost branch of the Squamata or as a sister group of Gekkota. Snakes have molecular ties with the Anguimorpha and Iguania (Townsend et al. 2004; Vidal & Hedges 2005; 2009; Wiens et al. 2012). The former was already suspected of being a close relatives of snakes but the second group neither includes limbless forms (Greer 1991) nor shows osteological links with snakes (Gauthier et al. 2012). Although many primitive fossil snakes are known (i.e. Rieppel et al. 2003; Zaher et al. 2009; Houssaye et al. 2011; Zaher & Scanferla 2012; Caldwell et al. 2015; Martill et al. 2015) they do not offer any solution to the problem.

Amphisbaenians (worm lizards) are among the most derived burrowing lizards (Kearney & Stuart 2004). Molecular analyses placed them far from snakes and dibamids (Townsend et al. 2004; Vidal & Hedges 2005; 2009; Wiens et al. 2012) within Lacertoidea, with the Lacertidae inside or next to them. Such their sister relationship was allegedly supported by the fossil Eocene *Cryptolacerta* (Müller et al. 2011). This lizard had a lacertoid skull but reduced limbs and other adaptations to fossorial life. That is why it was originally interpreted as the most primitive amphisbaenian and a link to the lacertids. I challenged its phylogenetic position (Chapter 3) proposing that it is the first known member of Lacertidae with reduced limbs but far from the amphisbaenian origins. Instead, I propose the Late Cretaceous *Slavoia* from Mongolia as the oldest and most primitive known amphisbaenian. It shows that the characteristic morphology of Lacertidae and Amphisbaenia evolved independently, but do not exclude their close relationships. *Slavoia* clarifies biogeography of the group, suggesting its
origins in Asia. Amphisbaenians probably used the land connections between Asia and other continents to disperse short after the end-Cretaceous crisis. The glaciations in the Neogene probably reduced their distribution as modern amphisbaenians are relicts on northern continents.

The postcranial anatomy of *Slavoia* is of special interest in the context of amphisbaenian limbless morphology (Chapter 4). Modern worm lizards have no limbs except for the Bipedidae, which retained forelimbs but lacks hindlimbs (Kearney 2002). The hand of *Bipes biporus* has equal number of phalanx (three) in each digit, the trait unique among lizards (Zangerl 1945). This implies a polyphalangy in the first digit (Fedak & Hall 2004), where the plesiomorhic count is two for all lepidosaurs (Kearney 2002). Because more basal amphisbaenians are limbless (Vidal et al. 2008) this raises questions about limb reduction in amphisbaenians. How many times worm lizards lost their limbs? What was the sequence of changes leading to their snake-like morphology? *Slavoia* had well developed forelimbs and not elongated body, but already had polyphalany in the first digit of the hand and reduced digits in the foot. This suggest that the reduction of hindlimbs was initiated before the body elongation and the split of the group into modern families, whereas forelimbs were lost several times independently. The presence of forelimbs and polyphalangy is probably a primitive trait in *Bipes biporus*.

The main conclusion from the review of data and their interpretation presented in this work is that paleontology may serve as an arbiter in controversies emerging at junction between molecular and morphological phylogenetic studies of extant lizards and rhynchocephalians. Only the fossil record provides truly independent measures to test hypotheses about evolution.