UCL RESEARCH DEPARTMENT OF CELL AND DEVELOPMENTAL BIOLOGY

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Dear Colleague

Please find attached report on the thesis submitted by Pavel P Skutschas for the Degree of Doctor of Biological Sciences, St Petersburg State University.

Yours sincerely

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Pavel P. Skutschas

Early stages in the evolution of salamanders (Lissamphibia, Caudata) and the transition from stem- to crown-group salamanders

Salamanders are represented today by ~650 species, but relatively little is known of their deep history. The earliest definite fossil salamanders date from the Middle Jurassic (~165 Ma) of Russia and Central Asia, China, and the UK, and include members of both stem- and crown-groups. Although there remains a large gap in the fossil record of salamanders, given that the earliest stem-frogs date from 250 million years ago, Jurassic stem-salamander fossils provide key information on ancestral salamander morphology. This, in turn, is relevant to fundamental hypotheses of salamander origins, but also to our understanding of lissamphibian origins and relationships, a contentious and highly debated topic within modern biology.

By far the most extensive early records of fossil salamanders come from the rich Jurassic-Cretaceous deposits of north-eastern China. A second set of salamander fossils – as yet only partly described – comes from Jurassic/Early Cretaceous deposits in Europe and North America. There are no obvious similarities between the Chinese and Euramerican salamander assemblages. Russian and Central Asian salamander specimens are therefore key to our understanding of early salamander relationships and palaeobiogeography as they have the potential to form a bridge between eastern and western assemblages. This material also provides important baseline anatomical information for those – like myself – working on salamander fossils from the other regions.

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General comments:

The thesis presents a summary and synthesis of Skutschas' seminal work on Jurassic and Cretaceous salamanders over more than a decade. Much of what we currently know about early Russian and Central Asian salamander material comes from Skutschas' work and publications over this period. Together they represent a novel and important contribution to the field.

Chapter review:

The thesis begins with a comprehensive overview of current knowledge of the salamander fossil record, especially in Russia and Central Asia, and of the significance of this knowledge to our understanding of salamander origins and relationships, as well as those of lissamphibians generally.

Chapter 1 reviews salamander skeletal characters, although it would perhaps have been useful to include some illustrations of postcranial as well as cranial characters.

Chapter 2 reviews current knowledge of stem-group salamanders from Britain, Russia, and Central Asia, with an overview of their skeletal characteristics. In their detailed descriptions of *Kokartus*, and the novel information on early salamander skull and long bone histology (with its implications for physiology), Skutschas and his collaborators have made an important contribution to our knowledge of these taxa.

Chapter 3 reviews ideas on the origin and relationships of Caudata, with a consideration of the similarities between karaurids and potential ancestral groups like the Permian branchiosaurs and *Gerobatrachus*. Of course, some of the similarities – especially with branchiosaurs – may be due to paedomorphosis. Moreover, although the atlas of *Kokartus* and *Karaurus* has an interglenoid tubercle – like *Gerobatrachus* and crown-salamanders – this feature is also present in stem-caecilians and albanerpetontids but absent in stem-salamanders like *Marmorerpeton* and 'salamander A' from the British Middle Jurassic. The polarity and homology of this character may therefore need further scrutiny. Moreover, new recently published data on albanerpetontid morphology raises questions about their relationship to batrachians, given the presence of elements like the supraoccipital and epipterygoids that seem to have been lost from the dissorophoid lineage at a much earlier stage.

Chapter 4 reviews what is known of the morphology (including histology) and relationships of early crown-salamanders, especially in relation to the long-standing (but weakening) vicariance hypothesis of Milner (1983) for the separation of cryptobranchoid and salamandroid salamanders. However, it should be borne in mind that the skeletal characters currently used to separate cryptobranchoids and salamandroids are limited, with undue emphasis on features like unicaptitate vs bicapitate rib-bearers. Moreover, some Chinese researchers consider the supposed salamandroid *Beiyanerpeton* to be a poorly preserved specimen of *Chunerpeton*.

Chapter 5 brings together the material in preceding chapters to present an overview of early salamander evolution – noting the similarities between Siberian and British salamander assemblages and the possible biogeographical implications of this. Of particular note are the Jurassic assemblages in Russia,

Kyrgyzstan and China in which relic non-lissamphibian temnospondyls are found together with salamanders – a co-occurrence currently unrecorded in western Laurasia. A second interesting and novel co-occurence (section 5.3) is that of apparently relictual stem- and crown salamanders surviving together well into the Early Cretaceous in Siberia. Given other 'Jurassic' features of the assemblage, this provides strong support for the hypothesis that this region may have acted as a refugium.

The final part of this chapter raises another important issue, linked to the question of cryptobranchoid vs salamandroid vicariance discussed previously, relating to the composition of Late Cretaceous Russian and Asian salamander assemblages up to – and across – the K-P boundary. As currently known (allowing for the new '*Bishara*' material) they are composed only of cryptobranchoids, raising questions a) as to the timing of arrival of salamandroids in this region and b) the phylogenetic position of the supposed stem-salamandroid *Beiyanerpeton* from China.

Assessment

This thesis, and the published work of the author that it summarises, represents a substantial body of novel and informative work carried out over more than a decade– either alone or in collaboration with colleagues. Through a combination of fieldwork, fossil description, histological analysis, and modern salamander skeletal biology, Skutschas has made a significant contribution to our understanding of early salamander evolution in Russia and Central Asia – a contribution that would be considered to meet the criteria for the Degree of Doctor in Biological Sciences at any institution.

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