Common origin and phylogenetic diversification of animal hormonal systems

D. Bückmann

Abteilung Allgemeine Zoologie, Universität Ulm, D–79 Ulm/Donau (Federal Republic of Germany)

The significance of the evolutionary history of hormones

The evolutionary history of hormones can contribute to our understanding of hormonal function. How does a compound become a hormone? The known animal hormones are members of different molecular groups, such as amines, peptides, steroids, juvenoids and iodinated thyronines. However, none of these groups consists only of hormones. There are amines, peptides, and steroids without hormonal properties. Evidently belonging to a certain chemical class of compounds is not sufficient for a molecule to be a hormone. To enable a compound to be a hormone a whole functional system is required, consisting of the compound itself, the hormone-producing tissue, the target organ, the primary effect of the hormone receptor complex and the final biological function. These factors together have been called the components of a ‘hormonal system’ by Karlson and Gersch.

There is a great variety of hormonal systems among metazoan animals, including man. The organs producing hormones and reacting to hormones have evolved from diverse other structures, which originally may have had other functions. They must have evolved in a way in which they always remained functional. Otherwise the organisms would have died out, and none of their progeny would exist today; only such progeny can be investigated physiologically. Therefore some properties of hormonal systems may just have historical causes, which cannot be understood without knowing their evolutionary history. An example for this is the history of the thyroid and its iodine-containing hormones as revealed by Gorbman and Barrington.

The evolutionary history of hormonal systems may be reconstructed by comparing the hormones of animals with various degrees of relationship, and tracing back the phylogenetic branches of animals with different hormones to common ancestors. In this way one can find out at what branching-point of the phylogenetic tree a change must have occurred. From what is known about animal evolution from fossils, one can even tell how many millions of years ago such an event took place. An impressive example for such a reconstruction is the history of the neurohypophyseal hormones as revealed by Acher.

In order to clarify the history of hormonal systems one could try to make a comparative survey of the hormonal organs, substances, and functional systems. All these components must have coevolved in such a way that the whole...
system remained functional. Therefore one might expect that a comparative study of the hormones, the hormonal organs, the target organs and the biological functions might all point to phylogenetical systems identical to those of the animals. Surprisingly, this was not the case, when whole animal classes and phyla were compared\textsuperscript{11,12}. There were rather certain rules as to the extent of diversity between the glands, the chemical compounds, and the functions in different animal groups. From these rules conclusions could be drawn on the phylogenetic age of the differences between those components, using the method outlined above. This method led to the conclusion that the peripheric epithelial hormonal glands releasing nonpeptide hormones must have evolved late in metazoan evolution, after the branching-off of the main animal phyla, and independently in each of them\textsuperscript{12,51}. This result was challenged immediately\textsuperscript{12}. It was not so attractive as an explanation involving one general developmental step common to all animals would have been. A monocausal hypothesis explaining every development by the same general principle is always the most attractive. Equally attractive is the picture of the evolution of physiological mechanisms from primitive ancestors continuously reaching higher levels and arriving at their most evolved state in the human species. This picture has severely hampered progress in comparative endocrinology. It did not allow invertebrates to possess other hormonal systems than vertebrates. When, in insects, the search for sex hormones like those in mammals remained without success, it was generally believed that invertebrates do not possess any hormones at all, though already in 1917 and 1922 Kopec\textsuperscript{39,40} had claimed that the insect brain might have a similar function to the vertebrate thyroid in promoting metamorphosis. In fact this was the first example of neurosecretion. However, he could not prove his results sufficiently and there was no general scientific concept into which they would have fitted. So his work was not taken notice of.

\textit{The approach of comparative physiology}

A new concept was provided by the idea that different animal phyla are not so much different in their level of perfection, but that they are constructed according to different principles. It is characteristic that the first book on comparative physiology, by von Buddenbrock 1928\textsuperscript{8} revived the discussion about insect hormones. From the concept mentioned von Buddenbrock concluded that hormones of other animal phyla might have functions different from those of vertebrate hormones\textsuperscript{14}. Hormones reach every body cell equally well and equally fast through the blood. They are well-fitted for synchronizing events in different and distantly located tissues. In order to find invertebrate hormones one had to look for such a synchronization. In vertebrates synchronization of sexual characters is necessary due to their periodical phases of reproduction, whereas in insects all the adult life is solely dedicated to reproduction. Therefore it is quite sufficient when the genetic mechanism of x and y chromosomes present in every body cell