Abstract Van der Klaauw was a professor of Descriptive Zoology in the period 1934–1958. This paper presents a concise annotated overview of his publications. In his work three main topics can be recognized: comparative anatomy of the mammalian auditory region, theoretical studies about ecology and ecological morphology, and vertebrate functional morphology. In particular van der Klaauw developed new concepts on functional morphology, based upon a holistic approach. A series of studies in functional morphology of Vertebrates by his students is added. An overview of recent morphological and theoretical studies show that this new approach had a long lasting impact in studies of functional morphology.

Keywords Comparative anatomy · Tympanic region · Ecology · Ecological morphology · Functional morphology

1 Introduction

In 1994 the Zoological Laboratory of Leiden University, home of the newly established Institute of Evolutionary and Ecological Sciences (IEES), was renamed Van der Klaauw Laboratory. This was done in honor of C.J. van der Klaauw (1893–1972), professor of Descriptive Zoology and director of the Zoological Laboratory in the years 1934–1959. Several lines of research were initiated and stimulated during his directorate: histology, ethology, ecology and theoretical biology. He spent most of his scientific life at Leiden University. His main own work was in animal morphology, but he made significant
contribute contributions to other fields, in particular to that of theoretical biology. He was one of the founders of the *Jan van der Hoeven Stichting voor Theoretische Biologie* (the Jan van der Hoeven Foundation for Theoretical Biology) encompassing philosophy of biology and methodology, and mathematical biology; v/dkl 641. This foundation publishes the journal *Acta Biotheoretica* and in the past the Bibliotheca Biotheoretica. Van der Klaauw was also one of the founders of the Museum for the History of Science in Leiden, now the Boerhaave Museum; he published several papers about items from the museum (v/dkl 54, 65, 67, 70). In this overview his main scientific contributions will be summarized and the impact on later work of other researchers reviewed.

A concise overview of his career can be found in Boschma (1958) and Brongersma (1972). Van der Klaauw was born in Amsterdam on November 16th, 1893. He studied biology at Leiden University, where he defended his PhD thesis in 1922. He was appointed assistant in 1919, curator in 1922, external university teacher in 1923, reader (associate professor) in 1931 and full professor in 1934, respectively. During the war he was taken hostage by the German occupying government. He retired in January 1959, but kept writing scientific papers. In 1947 he was appointed member of the Royal Dutch Academy of sciences.

Lately things have been changing in Leiden; the IEES has been incorporated in the newly established Institute of Biology and will be leaving the Van der Klaauw Laboratory shortly. It was the last natural science building in down-town Leiden. This moment seems appropriate for an evaluation of the contributions of van der Klaauw to our knowledge and understanding of various fields of biology.

### 2 Important scientific contributions

Van der Klaauw was in the first place a morphologist with a special interest in craniology. In his public lecture accepting the position of reader he discussed the place of morphology in biology (v/d kl, 37). After an overview of biological subdisciplines in relation to morphology he states that opinions diverge about the question what should be considered to belong to morphology. Van der Klaauw recognized that morphology has mainly a propedeutic significance for other biological subdisciplines. As such it will always be valuable for these areas. As for morphology in its own right he considered comparative anatomy to be the dominant field with emphasis on typology in an idealistic sense. Much of the work of van der Klaauw is characterized by a typological approach, even when he enters the fields of ecological and functional morphology.

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1 The papers of Van der Klaauw will be referred to as v/dkl + the number of the corresponding publication, thus: v/dkl 1 (his first publication).
Later on Van der Klaauw wrote the introductory chapter in the Dutch *Textbook on Comparative Anatomy of Vertebrates* (v/d kl 73). In this introduction he distinguished six morphological subdisciplines: descriptive anatomy, comparative anatomy, functional anatomy, ecological morphology, ontogeny and architectonic (*Bauplan*)- or synthetic morphology. We will consider several of these subdisciplines in the context of Van der Klaauw’s scientific work. He did not mention an evolutionary morphology. This does not imply that Van der Klaauw denied the importance of evolutionary theory. He concludes his introduction with the statement that the future program for morphology should be ‘the phylogeny of the architecture (building plan) of the form, which should be considered together with the function as an unity’. In his opinion, however, evolutionary theory had not yet explanatory power in morphology.

Van der Klaauw’s contributions to the field of morphology concerned several topics. His early work focused upon the tympanic region in mammals. A second subject concerned the basics of ecology and ecological morphology. In the third place he laid down the principles of functional morphology that were later elaborated by Dullemeijer and his coworkers (Leiden school of morphology, see Dubbeldam et al. 1989). The importance of Van der Klaauw’s contributions has also been recognized by other scientists. For example, in 1993 Hanken and Hall published a 3-volumes book about the skull; references to work of van der Klaauw are found in several chapters dealing with different aspects of skull morphology (v/dkl 6, 35, 77, 78, 84, 87, 100). The three topics mentioned above will be reviewed concisely in the following sections; also the impact of his work on later and current research will be considered.

Finally, Van der Klaauw produced hand-outs about his lectures on zoomorphology. After his retirement he published part of these lecture notes. So, finally we will have a short look at these notes as these are characteristic for the systematic approach Van der Klaauw used in his scientific work and teaching.

Van der Klaauw was not only a zoomorphologist, but also had great interest in theoretical issues in connection with the schools of morphology, in particular those of Lubosch and Meyer-Abich (e.g., v/dkl 38, 39, 55). This aspect has been discussed before (Trienes 1988). Trienes argued that van der Klaauw developed his concept of holistic biology influenced by, and in confrontation with the German school of idealistic morphology of Lubosch and Meijer-Abich. The holistic approach led in the long term to the theory of functional components thus offering an alternative to the reductionist experimental approach. We will not repeat the argumentation of Trienes, but indicate the development in van der Klaauw’s thinking in the following sections.

### 3 Studies on the bulla auditiva and neighbouring structures

The first line of research was a continuation of the work of his professor (van Kampen, 1905) and concerned the auditory region of the mammalian
skull. At that time comparative anatomy was a dominant scientific field. The main question concerned the homology of anatomical elements throughout the classes of Vertebrates. The auditory system of the mammals, including the status of the ossicles and other bony elements were subject of many studies (refs in v/dkl 8). Van der Klaauw participated in the discussions (e.g., v/dkl 6, 8.). His most important contribution, however, concerned the ventral bony wall of the cavum tympani, i.e., the bulla auditiva or bulla ossea. Van Kampen compared this region in a series of adult mammals. Van der Klaauw focussed on the ontogenetic development of this region thus adding a new set of data (v/dkl 3). Later on he expanded his research into the field of phylogeny studying fossil skulls. We will have a short look at both aspects.

3.1 Ontogeny of the bulla auditiva

The bulla auditiva had already been studied by several authors (see v/d kl 3). The central question concerned the homology of the bony elements of the mammalian auditory region with elements in the reptilian skull. Several elements contribute to the formation of this bulla, such as tympanicum, petrosum, alisphenoid, basisphenoid etc. (v/dkl 66, 74). In some mammals, however, the ventral wall is formed (in part) by a separate element, the entotympanicum. If this ventral wall in mammals is considered a new formation, the question rises whether the entotympanicum is also a new element and not derived from elements already present in reptilian ancestors. On basis of his comparative studies van Kampen (1905) had concluded that the entotympanicum was a new element without a homologon in the reptiles. Some of his considerations: the entotympanicum appears late in the ontogeny, it is hardly recognizable in Monotremata and Insectivores and only modestly developed in Marsupials. On account of his ontogenetic studies Van der Klauw (v/dkl 3) concluded that the entotympanicum consists ontogenetically of two elements, that he named the rostral and the caudal entotympanicum. The rostral part is initially part of the cartilage of the tuba auditiva. The caudal entotympanicum develops in the ventral wall of the cavum tympani, has a secondary connection with the tympanohyale and may be considered a derivative of Reichert’s cartilage. The caudal entotympanicum is assumed to form initially the ventral cover of the hind room of the cavum tympani. Only later on it participates in covering the ventral wall of the rostral part of the tympanic cavity. The contribution of the rostral and caudal parts to the entotympanicum differs greatly among the mammalian species and can be used as a characteristic to subdivide mammalian genera and families.

3.2 Phylogeny of the bulla auditiva

In the introduction of his impressive study on the bulla auditiva in fossil mammals van der Klauuw states that “his investigation .... on the development
of the auditory bulla in recent mammals ...taught me the importance of the tympanic region both in comparative anatomy and as a factor in the determination of the relationships of genera and larger groups” (v/d kl 35). The latter aspect is still an important issue in palaeontological studies of mammals (see below). The structure of this paper is characteristic for van der Klaauw: in about 290 pages he described presence, shape, size and other aspects of all elements of the bulla auditiva and surrounding area. Again and again he discusses systematically all aspects of each of the bony elements throughout the groups of recent and fossil mammals, thus surveying the data from the literature and incorporating own observations. In doing so he typifies the auditory bulla of the respective genera and families At the end he summarizes in 34 pages his own observations on the tympanic and entotympanic in 47 specimen belonging to 20 genera of fossil mammals. In several publications van der Klaauw provides data about other groups of fossil mammals (v/d kl 27–29, 36)

3.3 Impact of his work in recent studies

As said before, knowledge of the auditory bulla is used to establish relationships between groups of fossil mammals. In this type of studies one relies on previous studies as long as the original observations seem correct. In this context it is interesting to note that several recent papers concerning the auditory area in fossil mammals refer to the work of van der Klaauw. For example, Bloch and Silcox (2001), discussing newly found basicrania of Ignacius, and Gaudin and Wible (1999) about the entotympanic of Pangolins, refer to v/dkl3A and 35. The latter paper is also mentioned in among others Wiig (1985), Novacek (1985), Springer (1998), Ivanoff (2001), Meng et al. (2003), Horovitz and Sanches-Villagra (2003), Wible et al. (2001, 2004, 2005). Several papers on other skeletal elements refer to papers by van de Klaauw, e.g., Sanches-Villagra et al. (2002) and Wible (2003) mention the paper about skeletal elements in the in the tendon of the musculus stapedius (v/dkl 6). This overview does not pretend to be exhaustive, but serves to give an impression of the importance of the early work of van der Klaauw.

4 Ecology and ecological morphology

In the years 1935–1936 van der Klaauw published three theoretical papers on the relatively new field of ecology (v/dkl 59, 61 and 62). In 1948 a fourth paper about ecological morphology followed. He also presented his ideas to national (v/dkl 83, 90, 92) and international (v/dkl 85, 86) forums. The first point he wanted to make is that ecology as a new biological discipline is more than a simple form of natural history. The second is that this new area needs a set of concepts and definitions to give it a proper place in the array of biological disciplines. The aim of van der Klaauw was to provide (part of) this theoretical framework.
In the first of the series of papers van der Klaauw tackles the problem of the significance of the idea of teleology for the logic of ecology, reverting to the philosophy of Kant (v/dkl 59; also v/dkl 97). The central question is that of the teleological cause in the relation of organism and abiotic nature as well as in the relations between organisms (herbs and herbivores; prey animals and carnivores etc.). Van der Klaauw summarizes the views of Tschulok, Driesch and von Uexküll. Following Kant, van der Klaauw considers teleological explanations ‘as if’ explanations, i.e., as a matter of non-causal relations. He discusses the difference between autecology (Autökologie) and synecology (Synökologie), that is the ecology on the individual and the supra-individual level, respectively.

In the second paper van der Klaauw discusses a set of definitions beginning with those formulated by Haeckel (v/dkl 61). The subdivision of ecology into aut- and synecology is the topic of the third paper (v/dkl 62). The three papers have a strong theoretical character referring to many older publications, but with hardly any reference to practical research. As such, these papers may be useful to people interested in the early development of ecology as a biological discipline. However, the strong theoretical approach, the style of writing, and the fact that these papers are written in German may have diminished their accessibility for many researchers.

The fourth and final paper of this series (in English; v/dkl 77) has a different scope and character discussing the connection between morphology and ecology. In fact, Böker was the first to introduce the field of ecological morphology (references in v/dkl 77). It was defined as the study of the morphological features in connection with environmental factors. In the vision of van der Klaauw it concerns the relation between the size and shape of individual organisms and their surroundings (v/dkl 77). In autecology such a relation is teleological as the individual and its parts should fit the environment (adaptation; also v/dkl 59, 62). Van der Klaauw discusses extensively Böker’s approach pointing out that Böker ‘nowhere openly admits a teleological point of view’, which may be due to an interpretation of teleology as finality. Van der Klaauw goes on discussing the question whether the study of the morphology of the different organs also belongs to ecological morphology, as ecology regards whole animals and not parts of animals. His answer to this question is positive. Then, van der Klaauw formulates a series of questions about the relation between structure of organs and organisms, and the environment. Just to mention a few: By what qualities and characteristics does the structure fit the surroundings and to what degree does this interfere with adaptation? How does the structure of an organ fit the surroundings in which it performs its function? Do a number of organs cooperate to perform one function? What is the consequence of a certain function performed by one or a number of organs for other functions? Several of these questions already reflect the change of van der Klaauw’s thinking in comparative terms into thinking in functional terms. This part of his study is peppered with a large number of examples.

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Bock (1990) re-introduced the field of ecological morphology or—in his terminology—ecomorphology, referring to the work of Böker and van der Klaauw. He considers this a neglected area and notes that the paper of van der Klaauw (v/dkl 77) has been overlooked, even by the group of Leiden functional morphologists. Indeed, Dullemeijer did not mention these papers in his book on animal morphology (Dullemeijer 1974). Even though around 1980 a group Ecological Morphology was established in Leiden, the ecology papers by van der Klaauw are not mentioned in their publications (e.g., Witte et al. 1983, Witte 1984). However, in a comparison of the methodologies of ecology and morphology Dullemeijer (1980) used the ecology studies of van der Klaauw.

Hagmeier and Stults (1964) casually mention v/dkl 77. After Bock, to my knowledge Liem (1993) was initially the only one to refer to this paper in a review of the ecomorphology of the teleost skull. Lately, interest in ecological morphology and in van der Klaauw’s contribution has increased (e.g., Breda et al. 2005).

5 Functional morphology

5.1 A new approach in morphology

The most important contribution of van der Klaauw is the introduction of a new approach in functional morphology. His most influential papers may be those introducing new concepts in functional morphology (v/dkl 78, 84, 87), as well as that about the cerebral skull and facial skull (v/dkl 72). During the war 1940–1945 van der Klaauw was taken hostage by the occupying German authorities and spent some time in the German civil concentration camp St Michielsgestel (The Netherlands). He used this time to write a survey of the data on the Vertebrate skull from the literature. This resulted after the war in the series of papers on the architecture of the skull (v/dkl 78, 84, 87). In these papers van der Klaauw introduced two new cohering concepts. The first one is that of the functional component. Skeletal elements together performing a specific function should be considered as a unit with a certain degree of independence. The second concept is that of holism: the various functional components should fit together within the whole of the skull. For the latter aspect van der Klaauw may be inspired by the book Holism and Evolution (Smuts 1926). Van der Klaauw was able to make the concept of holism operational by introducing the functional component in functional morphology. In his paper on the distinction of the facial skull and the cerebral skull he considered these as relatively independently varying units. Initially, he used the term functional component for cranial elements, later on the weak parts were included. From 1950 on he started with his students a series of studies about the head anatomy of fishes, birds and mammals including the weak parts. Many of these studies resulted in publications (see: list of publications by students communicated by Van der Klaauw). However, even though the
approach was a functional morphological one, the functional interpretations were mainly based on observations in dead animals.

5.2 Impact of his papers on functional morphology

The concept of the functional component was rather loosely defined by van der Klaauw. However, he laid the foundation, on which his student and successor Dullemeijer could build the theoretical framework of the functional morphology in a holistic context. Moreover, Dullemeijer introduced the functional analysis in life animals as part of functional morphological studies. For details of his contributions, see Dullemeijer (1974), Dullemeijer and Zweers (1997), and Dubbeldam et al. (1989) and the references therein. From 1960 the Leiden functional morphology was a thriving research area, internationally known as the Leiden school of functional morphology. The importance of the approach of van der Klaauw has been recognized by many researchers in various fields of morphology (e.g., Hanken, 1983; Cheverud, 1982), though not everybody was convinced. Thus Gans (1969) preferred the term mechanical unit over functional component. Liem (1989) used the term functional unit in a comparable way. The main difference is that the term unit implies a sharply bordered element, whereas functional components more or less fade into each other depending upon the influence of the function. Most influential in favor of the ideas of the ideas of van der Klaauw was the American orthodontist Moss who introduced the concept of the functional matrix in orthodontics (Moss and Young 1960). This concept rests upon the same assumptions as that of the functional component. Through the papers of Moss and his coworkers other researchers discovered the work of van der Klaauw, and recognized its significance for their own research, e.g., Radinsky (1985), Anton (1989), Tollaro et al. (1994), Dressino and Pucciarelli (1997), Carlson (1999), Perlyn et al. (2001), González-José et al. (2005), and Kikuchi (2005). The papers were mentioned in several chapters in Hanken and Hall (1993) and were also the subject of a recent theoretical analysis (Dressino and Lamas 2003). Even though the term functional component is hardly used anymore, the holistic approach of van der Klaauw still has a place in functional morphology of the head, as well of other systems (e.g., Adams 1998).

Van der Klaauw’s last contribution to functional morphology was still more typology than functional morphology. In an extensive study he provides an exhaustive enumeration of types of muscle attachments and related specialization of skeletal areas of attachments (v/dkl 100). Even so, the paper proved to be useful to several authors, e.g., Anton (1999) and Zusi (in Hanken and Hall, 1993).

6 Lecture notes

It was already mentioned that Van der Klaauw prepared hand-outs with lecture notes for his students. These notes have a strong theoretical character
and are interlarded with numerous examples offering references to anatomical data. His style of writing is exemplified in his last publication (v/dkl 104), more or less an English version of these notes. This paper was preceded by another theoretical study (v/dkl 103). This paper consists of thirty-one statements, in which van der Klaauw expressed his opinion about the importance of the philosophic backgrounds of the biological sciences. After completing these papers van der Klaauw was unable to continue his scientific activities because of serious health problems. Therefore, it is gratifying to note that these papers also have found their way in the more theoretical literature (e.g., Liem 1967; Sattler 1984; Young 1993).

7 Concluding remarks

Van der Klaauw published about several other topics, among others about theoretical issues (e.g., v/dkl 38, 39, 45, 64) and historical issues (e.g., v/dkl 33, 41, 46, 54, 58, 65). However, his most important contributions were in craniology. But here too, his contributions have a different weight. Whereas the references to his publications on the auditory region have to do with observations in specific species, have those on functional morphology a more fundamental and lasting impact on the methodology in functional and evolutionary morphology. As for ecological morphology, the connection between morphological features of the organism and the environment is often implicit in functional morphological studies.

In his capacity of director of the Zoological Laboratory of Leiden University, van der Klaauw had a long lasting impact on the development of this institute. He initiated several new lines of research e.g., theoretical biology, histology. During his director Tinbergen began his studies in Ethology, Kuenen in Ecology. The short overview of the present paper shows that he was not only an inspiring teacher and an able administrator, but also a gifted scientist, who opened new vistas, in particular for functional morphology. The laboratory bearing his name may disappear, his merits will still be recognized for some time.

8 Appendix 1

Papers By Van Der Klaauw

1921

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9 Appendix 2

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