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African dwarf-crocodile scale-counts evaluated as supporters of *Osteolaemus tetraspis osborni* (Reptilia, Crocodylia, Crocodylidae)

by

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Submitted in fulfilment of part of the requirements for the degree

of Master of Science in Wildlife Management

in the Faculty of Natural and Agricultural Sciences

University of Pretoria, Republic of South Africa

Supervisor: Prof. W. van Hoven

2010

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DECLARATION

I, Rogier de Boer, declare the dissertation, which I hereby submit for the degree of Magister Scientiae (Wildlife Management) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this of any other tertiary institution.

Signature:

Date: 26 – 01 – 2011

PREFACE

All of the new data reported in this thesis was collected in Africa during a 2006-2007 field-work expedition called the Roland Zoer *Osteolaemus* Project. The project leader fully supported the preparation and expedition time required for the scalation studies reported here. Thus, although all of the project members participated in the counting of scales on African crocodilians, it was always clear that the final responsibility for reporting these scalation characters was assigned to Rogier de Boer.

No crocodiles were physically hurt or killed by the Zoer 2006-2007 *Osteolaemus* project. No crocodile habitat was degraded or destroyed. The expedition did not encourage or pay any local people to catch or kill any wild crocodilians. However, local guides were sometimes employed when travel on foot through the equatorial rainforest at night was necessary.

No physical specimens (neither whole animals nor parts and derivatives) were collected during the course of this scalation study. However, the 2006-2007 expedition was also studying DNA variation (as part of an international research project), and was thus covered by national permits issued to Roland Zoer for all situations where C.I.T.E.S. regulated crocodilians were being handled.

After several years of preparation, five young men from the Netherlands were able to collect data in the equatorial rainforest along the Atlantic coast and also inland in central Africa. Three of the researchers did the first part (roughly half) of the travel, and then two returned home by air, and were replaced by two others who flew-in to complete the task. The transfer of data-collecting duties (from the first team to the second) happened on schedule, and thus all of the scalation (dorsal and ventral) was recorded by people with exactly the same preparation for answering questions in the expedition’s protocol. The leader of the expedition, Mr. Roland Zoer, did the whole journey from South Africa to the Netherlands by land, and was the owner of the field-work vehicle.

Before the expedition, in the Netherlands, Mr. Franklin Ross wrote the protocol, and instructed all five of the expedition members about the application and potential utility of the Ross + Mayer (1983) method, and also the expedition protocol included many other kinds of characters, including cranial morphometrics. Later, the actual field-work included practice at answering the protocol (including measuring the total length of the animal, and sexing it, and samples for DNA analysis) on many crocodiles in southern Africa (R.S.A., Botswana and

Namibia) including mostly Nile crocodiles, but also a few African slender-snouted crocodiles, and one important specimen of *Osteolaemus* that had earlier originated in the bushmeat market at Kinshasa, Democratic Republic of Congo, back in the mid 1980's. Although a very few Nile and slender-snouted crocodiles, *Crocodylus niloticus* and *Crocodylus cataphractus*, were examined in the central part of West Africa, the expedition's primary focus was the African dwarf-crocodile, *Osteolaemus tetraspis* Cope, as two subspecies.

The 2006-2007 field work was successful at gathering data from both sides of the subspecies boundary between *Osteolaemus tetraspis tetraspis* Cope, and *Osteolaemus tetraspis osborni* (Schmidt). The dedication that was needed for completing the sometimes dangerous and uncomfortable field-work was inspired by the generous encouragement of many individual people and organizations, with special appreciation to the professional biologists listed in Figure 0 (below), who substantially and significantly contributed to the expedition's preparation.

- Dr. Wouter van Hoven Professor/Director of the Centre for Wildlife Management, Univ. Pretoria, R.S.A.
- Dr. Fritz W. Huchzermeyer Veterinarian, at Onderstepoort Veterinary Institute, R.S.A. and Vice Chairman of Veterinary Science of the Steering Committee of the Crocodile Specialist Group (CSG).
- Dr. Terry Cullen Director and owner of the Cullen Vivarium Conservancy, Milwaukee, Wisconsin, USA (CSG).
- Dr. Llewellyn D. Densmore Professor and Associate Chair, Department of Biological Sciences, Texas Tech University, Lubbock, Texas, USA (CSG).
- Dr. J. Perran Ross recently Executive Officer of the I.U.C.N. Crocodile Specialist Group, now Associate Scientist, Dept. Wildlife Ecology and Conservation, Univ. Florida, Gainesville, Florida, U.S.A. (CSG).
- Dr. J.W. (Pim) Arntzen Acting Curator of Reptiles and Amphibians at Naturalis (NNM), Leiden, the Netherlands.
- Mr. Franklin D. Ross guest researcher at NNM (the National Natural-history Museum), Leiden, the Netherlands.

Figure 0 Chronological list of academic biologists who contributed to the preparation of the 2006-2007 expedition

CSG = Active member of the Crocodile Specialist Group of the I.U.C.N. The two persons who have been most closely involved in the later organization and writing of this thesis are Prof. W. van Hoven as my academic supervisor, and in a sense equally F.D. Ross as an author of the Ross + Mayer (1983) paper which is basic to this study, and as the originator of the expedition's protocol. Here, I gratefully express my personal appreciation to both of them for their steadfast support and shared scientific ideals.

In addition to the scale-counts and cranial morphometrics studied by the expedition, the field-workers also recorded the sex of the animals. Sex is a possible alternative to geography as an explanation for any results that appear to correlate with the C.I.T.E.S. prediction of two essentially allopatric *Osteolaemus* subspecies. In contrast, although reported in two tables in Chapter 1, the total length of the individual African dwarf-crocodiles is a variable that has no causal connection to the scalation data analyzed in this thesis. As a general rule, the scale-counts on baby crocodilians remain the same results as they will be when the individual animal grows to maturity (Ross + Mayer, 1983:313).

Finally, I most sincerely thank my four other expedition members of the 2006-2007 *Osteolaemus* project: Mr. Roland Zoer (project leader), Mr. Jeroen Koorevaar, Mr. Stefan van Lieshout and Mr. Daniël Peereboom. It was only with the help and hard work from each and every member that the expedition became the success that it is.

Rogier de Boer

October 2009

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CHAPTER I INTRODUCTION: WHY THIS STUDY, AND HOW IT WAS DONE (on three species of African crocodilians)

Figure 1.1 Two prefatory notes

Two potentially confusing place names (the nation of Congo, compared with the Democratic Republic of Congo) are avoided in this thesis by attaching the capital city of Congo to the nation's name, producing the hyphenated national name "Congo-Brazzaville" or "Congo-B" for one, while in contrast the Democratic Republic of Congo (D.R.C.) has been given the national title of "Zaïre-DRC" because in recent times the DRC nation was called Zaïre. The capital city of Zaïre-DRC is Kinshasa, which is located on the eastern bank of the Congo River, while the capital of Congo-Brazzaville is located near Kinshasa, but on the western bank of the Congo River.

One fundamental assumption in this thesis is that all of the Ubangi River and its tributaries (including Likouala River), and also the Congo River immediately north of Kinshasa and Brazzaville cities, is all in the geographic range of one subspecies, *Osteolaemus tetraspis osborni* (K.P. Schmidt, 1919). In contrast, this thesis defines all of the African dwarf-crocodiles along the western coast of Africa, from the bridge that crosses the lowermost Congo River and then extending northward and westward to Senegal, as *Osteolaemus tetraspis tetraspis* Cope, 1861. This geographic division between the two subspecies was for many decades the intention of the Wermuth + Fuchs (1983) range map and written distributions adopted by C.I.T.E.S..

1.1 INTRODUCING A NEW METHODOLOGY AS A TOOL THAT COULD HELP TO RESOLVE AN OLD PROBLEM

The original Ross + Mayer (1983) study at Harvard University was limited to museum specimens. In contrast, this University of Pretoria Master's thesis is based on field-work, and is probably the first major application of the Ross + Mayer (1983) technique and methodology to a wild crocodilian population, testing for geographic variation at the subspecies taxonomic level.

Exactly why the Convention on International Trade in Endangered Species (C.I.T.E.S.) has not adopted the F.D. Ross & G.C. Mayer (1983) method and conclusions, or even any raw data from Ross + Mayer (1983), is a mystery. One factor could be that although Dr. Eberhard Frey (1988a + b) found the Ross + Mayer (1983) paper to be the correct model for the body (thoracic, lumbar and sacral) and tail (caudal) sections of an American alligator, the interpretation of the *Alligator mississippiensis* neck scales in Frey (1988a + b) was wrong. Thus, because Frey (1988a + b) employed cervical (neck) numbers that resembled (in error) the earlier (and correct) Ross + Mayer (1983) cervical numbers, the neck conclusions in Frey (1988a + b) created controversy.

In the Netherlands, in 2005-2006, Mr. Franklin D. Ross, an author of Ross + Mayer (1983), and an advisor to the Zoer *Osteolaemus* project, divided the expedition's study of African crocodilians into three parts. The expedition leader, Mr. Roland Zoer, did animal length and sex, and collected DNA and other tissue samples. Detailed cranial measurements were made by Mr. Jeroen Koorevaar, and scale-counts were performed by the author of this thesis, Mr. Rogier de Boer. Thus, the three scientists were separated intellectually from each other by each man concentrating on an individual specialist responsibility. Each of the three expedition members performed an integral and necessary part of a whole biological investigation, and thus the expedition had (and has) the potential of contributing in three complimentary ways toward solving the most urgent African crocodile systematic problem that faces C.I.T.E.S. today.

1.2 WHY SCALES ON AFRICAN DWARF-CROCODILES WERE COUNTED: THE C.I.T.E.S. STORY ABOUT *OSTEOLAEMUS* AND ITS TWO CURRENT SUBSPECIES

When Karl Patterson Schmidt named a type and two paratypes as *Osteoblepharon osborni* K.P. Schmidt, 1919, new genus and new species, Schmidt (1919) made a wild guess. One of the three specimens exhibited an unexpected character, and this character had always been a generic character, so even though there was difficulty in perceiving these three African dwarf-crocodiles as even a subspecies based on all other characters, the Schmidt (1919) sample of dwarf-crocodiles received a genus of its own, in honor of Dr. Henry Fairfield Osborn, Director of the American Museum of Natural History (A.M.N.H.), who raised the money to send the explorers Chapin and Lang to travel the Congo River from its mouth (at Banana on the Atlantic coast) to the far interior of the continent at the Ituri Forest in the northeastern corner of today’s Democratic Republic of Congo (the DRC, recently temporarily known as Zaïre, but called the Belgian Congo in 1919).

Because it was based on a single character that is quite possibly variable within the type series of three specimens, *Osteoblepharon osborni* Schmidt was to some degree a patronage taxon. It was impossible for the scientific world to ignore an A.M.N.H. publication, and if the three specimens from the Ituri Forest (northeastern corner of Zaïre-DRC) did pass the test of time as a new genus and new species, then the name of Dr. Osborn would become immortal and find its way onto the regulated species list when C.I.T.E.S. was later signed into law in the early 1970’s. Alternatively, if *Osteoblepharon osborni* Schmidt did not pass the test of time, then Osborn’s name would be listed in synonymy, and yet still be remembered.

When K.P. Schmidt named what has become today’s subspecies *Osteolaemus tetraspis osborni* (Schmidt), which today is on the C.I.T.E.S. list, Karl Schmidt was a fairly young man who later moved from New York City to Chicago, Illinois, at the Field Museum of Natural History, and had a lengthy and distinguished career in crocodile nomenclature and systematics, revising several groups of living crocodilian species and with papers about crocodile fossils as well. It is probable that if Schmidt had not become such a respected name in crocodile and other reptile studies, then the history of *Osteolaemus tetraspis osborni* (Schmidt) would be shorter. However, science has progressed slowly, and thus for a while there was *Osteolaemus osborni* (Schmidt), as a species, because it was generally unthinkable that K.P. Schmidt could be entirely wrong.

In the early 1970's when the C.I.T.E.S. list was being assembled, the various major political opinions (notably the United States, England and Germany) agreed that Schmidt's Ituri Forest specimens were not worthy of a genus, and further that they were not worthy of being a species. However, keeping the name (*osborni*) on the list as a subspecies was considered the right thing to do, because essentially all that was known about the dwarf-crocodiles in the Congo River interior of Africa, and especially the Ubangi River drainage in the northern part of Zaïre-DRC, was from the original Schmidt (1919) publication, which included some very interesting geographic distribution remarks written by the collector of the specimens, Herbert Lang. Part of the hesitancy to drop Schmidt's dwarf-crocodile from the active list was that in 1948, Dr. Robert Inger at the Field Museum (F.M.N.H.) in Chicago thought that a scale-count character was diagnostic for *Osteolaemus tetraspis osborni* (Schmidt).

To strengthen the case for *Osteolaemus osborni* (Schmidt), the 1919 type description of the genus and species had made an effort to distinguish the new 1919 taxon from *Osteolaemus tetraspis* Cope, 1861, by means of selected scale-counts on the animal's neck. Later, when Inger (1948) demoted *Osteoblepharon* Schmidt, 1919, to become a junior synonym of the older genus *Osteolaemus* Cope, 1861, the paper by Inger reviewed Schmidt's cervical scalation character (the post-occipital scales) and found it to be lacking in merit, but Dr. Inger believed that the available sample of African dwarf-crocodiles from throughout their geographic range indicated that a different scale-count character (the double-crested caudals) might work. Thus, according to Dr. Inger's model of two allopatric species in the genus *Osteolaemus* Cope, the Atlantic coastal *Osteolaemus tetraspis* Cope taxon has a low and uniform number of double-crested caudals (DCC's), while in contrast the interior *Osteolaemus osborni* (Schmidt) species from the Ubangi River, and also the Congo River above Kinshasa, has a higher and more variable number of DCC's (see below in Chapters 5 and 6 for details about this character, and for Dr. Inger's DCC data).

When Inger's two species were reduced in taxonomic rank to be merely two subspecies, the hypothesis that their double-crested caudal (DCC) scale-counts were diagnostic for separating the two taxa stayed with them. This dorsal scalation character, as Inger (1948) remarked, was based on a very small sample. However, it has remained untested until Chapter 6 in this University of Pretoria Master's thesis. The highest priority for C.I.T.E.S. in the early 1970's was the regulation of commercial belly-hides which generally do not have their double-crested caudal scales (DCC's) present. There was a hypothesis from King + Brazaitis (1971) and Brazaitis (1973) (based on museum specimens in New York and Washington) that the two subspecies of African dwarf-crocodiles could be distinguished from each other by the number of transverse rows of ventral scales crossing the belly between the throat-collar and the obstruction surrounding the cloacal opening (the collar-vent = C-V character), which is the subject of Chapter 4 in this thesis, and it too is tested with a large and relevant sample of wild animals for the first time, here in this thesis.

The only character that originally justified the genus *Osteoblepharon* Schmidt, 1919, was the absence of the complete bony nasal septum (the division between the two nostrils is partly cartilage in *Osteoblepharon osborni* Schmidt) at least on one Ituri Forest adult specimen, compared with the type description of *Osteolaemus tetraspis* Cope, 1861, which said that one skull, without locality data (other than "western Africa") had a completely ossified internarial septum. The genus *Osteolaemus* Cope was based on the species *Osteolaemus tetraspis* Cope, with two type specimens. One was the cleaned skull without precise data. The other was a dorsal skin, from the Ogowe River in Gabon, which is the official type locality, even though the skull could possibly have been from some place other than Gabon.

The details about the neck scales in Cope (1860:549-550), which is the bibliographic citation for the type description of *Osteolaemus tetraspis* Cope, 1861 (the scientific name on p. 549, and the title of the paper on p. iv, became available in early 1861), had apparently not been read by Schmidt (1919), so the original idea that the interior (Ituri Forest = Ubangi River and Congo River down-stream to Kinshasa) taxon was externally distinguishable by neck-scales from the coastal taxon (type locality Ogowe River in Gabon) was to some degree a waste of time. The post-occipital scales on the neck of the African dwarf-crocodile are the subject of Chapter 2 (below), where today's revised hypothesis is that no taxonomic differences in neck-scales will be found. However, the data in this thesis will be utilized to test both hypotheses, with an enlarged sample size. Similarly, Robert Inger's hypothesis about the number of transverse double-crested caudal rows (DCC's) being a non-overlapping cline will be tested with a much larger sample in Chapter 6, and of special interest to C.I.T.E.S. is the collar-vent (C-V) count on the belly skin, which is also a cline, and this C.I.T.E.S. character (ventral scale-counts) will be tested in Chapter 4 (below).

Knowledge about the amount of variation in the number and physical size and proportions of the nuchal scales of the cervical shield on the neck of the African dwarf-crocodile is expanded in several ways in detail in Chapter 3 (below), and with other characters in Chapters 5 to 7, which also explore the possibility that, when n=68, and when the sample crosses the subspecies boundary, some *Osteolaemus tetraspis* scale-counts could support the continued recognition of two subspecies of dwarf-crocodiles by C.I.T.E.S. However, if the scale-counts do not actually support the subspecies *Osteolaemus tetraspis osborni* (K.P. Schmidt), then the question goes back to the skull (Jeroen Koorevaar's potential University of Pretoria Master's thesis about cranial proportions), and the bony nasal septum character, and possibly also a new character involving selected aspects of coloration (Roland Zoer's potential wildlife Master's thesis).

If it should turn-out in the end that none of the Ross + Mayer (1983) characters in Chapters 5 to 8 are of taxonomic utility for dividing *Osteolaemus tetraspis* into two subspecies, at least the experiment is repeatable. The same applies to the neck scales, and also to the collar-vent (C-V) count and a transverse count on the belly, all of which are defined more precisely in this thesis than probably ever before for any African crocodile species. Negative results (including the C.I.T.E.S. collar-vent and mid-belly transverse ventral scales characters) would not justify the dropping of the subspecies, because the head and some coloration characters (and DNA) have not yet been reported. However, scale-count data could possibly justify keeping Schmidt's taxon on the C.I.T.E.S. list, if any consistent and non-overlapping geographic variation results are evident. In addition to geography, this thesis also investigates sexual variation, which has never been done in the African dwarf-crocodile in the wild. No matter what the taxonomic results of this thesis are, the data is real. The characters in Chapters 2 to 8 are defined, the sample of *Osteolaemus* is large, and all of the data was collected consistently, with the same definitions, across the C.I.T.E.S. subspecies boundary.

1.3 THIS AFRICAN CROCODILE EXPEDITION IN 2006-2007 STUDIED THREE SPECIES, BUT CONCENTRATED ON *OSTEOLAEMUS*

The Roland Zoer *Osteolaemus* expedition traces its origin directly to Prof. Wouter van Hoven and also Dr. Fritz Huchzermeyer, both in the Republic of South Africa. Almost from the beginning, the focus of the study was narrowed from the Nile crocodile and other African crocodilians in general, to the specialized and restricted subspecies taxonomic problem in *Osteolaemus tetraspis* Cope, the dwarf-crocodile of equatorial western Africa. In 2004, the preparation and arrangements for the expedition across the African continent had already started. A considerable amount of literature on the subject was studied. This literature survey resulted in the project's research proposals. Two of the principal investigators (Rogier de Boer and Roland Zoer) visited a crocodile research institute in France and also the museum library in Paris. In this stage of the preparations the success of the project clearly depended on the availability of finances, and thus fund-raising for the African dwarf-crocodile project was an early priority.

In the autumn of 2005, two of the principal investigators (De Boer and Zoer) visited the Cullen Wildlife Vivarium Conservancy in Florida, U.S.A., for about five weeks. There, Dr. Terry Cullen instructed the two Dutch students in the correct procedures and methods for handling living crocodilians, and for drawing blood from them. While in Florida, additional advice about C.I.T.E.S. permits was received from Dr. James Perran Ross, recently the Executive Officer of the Crocodile Specialist Group of the I.U.C.N. (The International Union for the Conservation of Nature). Also, while in the United States, contact was made with Dr. Llewellyn Densmore in Texas, concerning DNA sampling techniques, equipment and procedures (including permits for international transport of tissue samples for DNA analysis).

Later, in 2005-2006, Mr. Franklin D. Ross (an author of the Ross + Mayer paper) instructed all five expedition members about the Ross + Mayer (1983) technique, and also about other aspects of gathering additional relevant data, involving each student receiving at least 14 hours of direct face-to-face science tutoring. These tutorials took place at the National Museum of Natural History, Leiden, the Netherlands, or alternatively at the personal library of Mr. Ross at his home address, also in the Netherlands.

Finally, when the funding for the project was complete, in April 2006 the crocodile expedition started off. The three principal investigators (Mr. Zoer, Mr. Koorevaar, and Mr. de Boer) travelled to Pretoria, South Africa by airplane, where they collected their pre-arranged expedition vehicle, and made additional preparations for the trip by car (a Toyota Landcruiser with official seats for two, modified to seat three people) across the Congo River and the western equatorial part of the African continent, crossing into Europe at Gibraltar, and eventually back to Amsterdam, in the Netherlands. During the time that the field-crew were in South Africa, the St. Lucia refuge and several private crocodile farms were visited, and many Nile crocodiles (and also a few other relevant crocodilian species) were examined, and thus the expedition members gained experience in filling-in the field protocols, and at the same time arrangements for visas to other nations were made.

Later during the actual expedition, two additional Dutch students (undergraduate honors in wildlife), Mr. Stefan van Lieshout and Mr. Daniël Peereboom, both of whom took the scale-counts data for Mr. Rogier de Boer during the few months following the return of Mr. Koorevaar and Mr. de Boer to the Netherlands on schedule (this was an originally planned change of field persons), were also instructed by Mr. Ross, and thus it happened that the five individuals that did the field-work on the Zoer 2006-2007 expedition had exactly the same definitions and names for crocodilian scalation characters, measurements, and other protocol subjects.

With three Dutch nationals in the car at all relevant times, field research on African crocodiles was conducted in numerous southern African and also western African countries. Research on the three African crocodile species in the 2006-2007 expedition was conducted in South Africa, Botswana, Namibia, the interior of Congo-Brazzaville (the Ubangi River drainage), the Kinshasa region in the interior of Zaïre-DRC, the coastal zone of Congo-Brazzaville, and in Gabon, Cameroon and Benin. An ecological survey was also conducted in Cabinda, which is *Osteolaemus* habitat, but no animals were examined.

Although research on crocodiles was conducted in the above-mentioned countries, some of the places of origin differ from the place where the animal was examined. The actual places of origin of the three African crocodile species examined by the 2006-2007 expedition are presented in Table 1.1 (below).

Table 1.1 Place of origin of three species of African crocodiles in the 2006-2007 expedition

General locality	Nile crocodile	slender-snouted	dwarf-crocodile	total animals
Benin	1	0	1	2
Botswana	56	0	0	56
Cameroon	4	0	33	37
Congo-B COAST	0	0	11	11
Congo-B INTERIOR	0	0	14	14
Gabon	0	1	8	9
Kenya	1	0	0	1
Namibia	1	0	0	1
South Africa	39	0	0	39
Zaïre-DRC	0	0	1	1
Zimbabwe	1	0	0	1
Unknown	0	2	2	4
Total	**103**	**3**	**70 (68 with data)**	**176**

This table shows the nation of origin of Nile crocodiles (*Crocodylus niloticus*), slender-snouted crocodiles (*Crocodylus cataphractus*), and African dwarf-crocodiles (*Osteolaemus tetraspis*) in the 2006-2007 crocodile total field-sample, presented in alphabetical order, and with Congo-Brazzaville divided into two categories.

All specimens examined by the 2006-2007 crocodile expedition were listed together in Table 1.1 (above). The Nile crocodile sample (n=103) will be presented in greater detail in Table 1.2 (below) and, the relatively small sample of African slender-snouted crocodiles (n=3) is detailed in Table 1.3 (below). Note that the African dwarf-crocodile sample actually contains 68 specimens instead of 70 animals, because two animals examined at St. Lucia, South Africa were earlier obtained from the Bronx Zoo, New York, U.S.A., and therefore were left-out of the sample. The distinction between African dwarf-crocodiles from the equatorial Atlantic Ocean coast, as opposed to animals from interior central Africa, will be explained in Subsection 1.5 (below), but first the Nile crocodile sample in Table 1.2 and some other details are presented.

Table 1.2 Geographic distribution of *C. niloticus* (n=103) examined in this 2006-2007 study

Country of origin	number of animals	locality where examined
South Africa	39	South Africa
Namibia	1	South Africa
Botswana	56	Botswana, and Namibia
Zimbabwe	1	South Africa
Kenya	1	Namibia
Cameroon	4	Cameroon
Benin	1	Benin

This table shows all Nile crocodiles (n=103 *Crocodylus niloticus*) in this Zoer 2006-2007 expedition sample examined at various different research localities, together with their places of origin. The Nile crocodiles examined in Namibia (at Otjiwarongo) all originated from the Okavango Delta, Botswana, except one *Crocodylus niloticus* that originally came from Kenya, and was also examined at the Otjiwarongo crocodile farm in Namibia. The animals that were originally from Namibia and Zimbabwe are specimens in alcohol that were examined at the Transvaal Museum at Pretoria, South Africa.

The knowledge gained while capturing, measuring, and counting the scales on *Crocodylus niloticus* in Natal and across southern Africa was important experience in preparation for field-work and also for examining captive animals later in the equatorial rainforest. However, although at least a thousand Nile crocodiles were available, the expedition considered the practice sufficient at approximately 100 living animals.

Nile crocodiles and African slender-snouted crocodiles were of general interest, but *Osteolaemus* was the primarily focus of the 2006-2007 expedition. The big disappointment was the small number of slender-snouted crocodiles (*Crocodylus cataphractus*) encountered, as detailed in Table 1.3 (below).

Table 1.3 Geographic distribution of *C. cataphractus* (n=3) included in the 2006-2007 total sample

Country of origin	number of specimens	locality where examined
Gabon	1	Ogowe Lambarene, Gabon
no data	2	St. Lucia, Natal, South Africa

The slender-snouted crocodile species was the smallest taxonomic sample from the 2006-2007 crocodile expedition in Africa. Just three (3) animals were encountered. The animal examined in Gabon at Lambarene was a stuffed specimen (no sex data), as opposed to the two living animals (both male and in captivity) which were in a reptile park at St. Lucia, South Africa. The range of variation in total length of slender-snouted crocodiles in this sample, being the average of the length taken from snout tip to tail tip measured above the animal, and the length measured below the animal on a flat surface, is 98 cm to 155,7 cm.

The two African slender-snouted crocodiles in the 2006-2007 sample examined in Natal at the St. Lucia Park’s captive reptile compound (public exhibit) lack information about the place of origin. Thus, only the one *Crocodylus cataphractus* specimen from Gabon had locality data. However, while in Africa, the 2006-2007 Zoer expedition was actually able to examine (and take complete protocols on) all three African crocodilian species, even though the sample of slender-snouted *Crocodylus cataphractus*, also sometimes known as *Mecistops cataphractus* (Cuvier), was small.

In review, the African nations visited by the expedition, are all mapped together in Figure 1.2 (below).

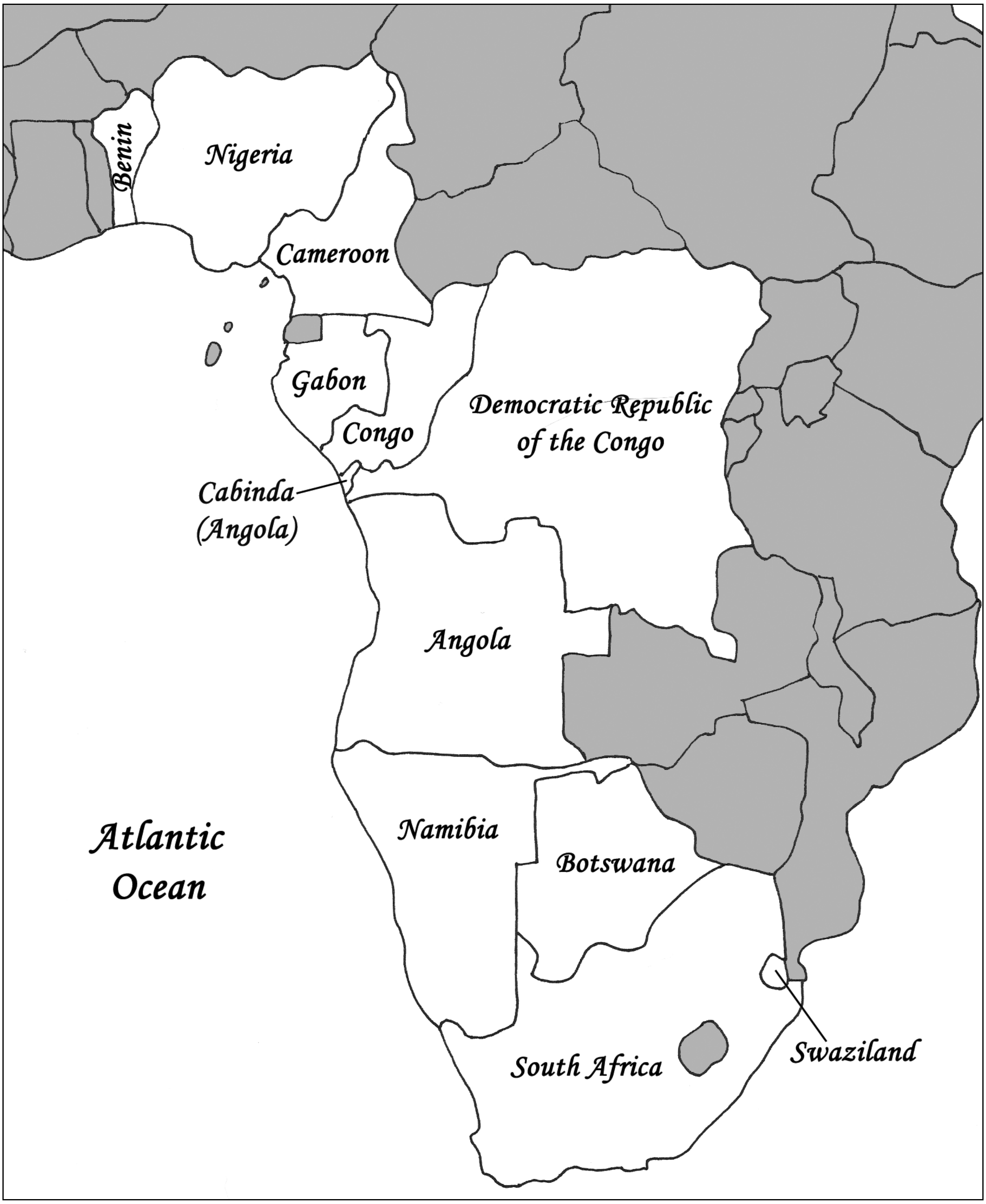


Figure 1.2 African countries visited during the 2006-2007 expedition

The African countries were visited overland by car, starting off in South Africa and going North via Botswana, Namibia, Angola, Democratic Republic of the Congo (DRC), Cabinda (Angola), Congo (Congo-Brazzaville), Gabon, Cameroon, and Nigeria to Benin. Some of the countries (Angola, Nigeria) were crossed without collecting field-samples on crocodiles. In the case of Nigeria, it was for safety reasons that the crew decided to cross very quickly.

1.4 SOME GENERAL NOTES ABOUT FIELD-WORK METHODS EMPLOYED IN THIS THESIS (INCLUDING THE PROTOCOL)

Research on the three African crocodile species was conducted in retile parks, on Nile crocodile farms, at local markets and along the side of the road (bushmeat), in museum collections, and also in the wild (captured, protocol done, and later released at original place). All living animals were handled and examined in the same manner following the expedition's research protocol (written specially for the Zoer 2006-2007 *Osteolaemus* project). The crocodiles were caught by hand or with the use of a catching pole. When caught the animal was immobilized by fixing the jaws closed with tape or elastic bands, restraining the front and back-legs with nylon cord, and by covering the animal's eyes with a towel and tape. The immobilized animal was then ready to be examined and measured. Note that no narcotics were administered to sedate the crocodiles handled for this 2006-2007 sample, thus reducing the risk of serious stress problems hurting the crocodile.

The scale counting and the skull measurements were done first, and later the blood samples, tissue samples, and cloacal swabs were taken. All of the investigators had their own specific tasks, and were assisted by each other while collecting data. Examples of the expedition's protocol are appended as Annexure B (below). Also, in addition to answering the actual questions in the field-protocol, drawings were often made and photographs were taken. In this way the answers to the questions from the field-protocol could often be compared with the drawings and photos to confirm (or clarify) any surprising results. Note that when it was necessary, the dorsal surface of the scales on the neck was cleaned to get a clear view of the edges of the individual scales involved in the neck-shield.

Sex was determined (= examined) on all possible specimens in the 2006-2007 crocodile expedition. Sex of the specimens was determined by means of the Brazaitis finger in-the-hole method ("probed") by Mr. Zoer and, as a second opinion, by one of the other principal researchers. So, sex is known on all individuals in this sample that could be probed.

The Zoer 2006-2007 sample of *Osteolaemus* does not include any nests of siblings (brothers and sisters with the same genetics). The same was probably true about the Bronx Zoo (King + Brazaitis, 1971; and, Brazaitis, 1973) sample; and, also true about the Robert Inger (1948) sample (including part of the original Schmidt, 1919, sample). However, in theory, a study could possibly have a high n (n=12, for example or n=24 even) that is actually one father's and one mother's offspring, or the parents and their children. Thus, with no pods of siblings, nor parent and offspring associations in the Zoer 2006-2007 sample, the genetic diversity represented is good (= the maximum).

1.5 THE 2006-2007 AFRICAN DWARF-CROCODILE SAMPLE (N=68 WITH LOCALITY DATA) DIVIDED INTO COAST AND INTERIOR TAXA

As noted earlier, neither Nile crocodiles nor African slender-snouts are the real subject of this thesis. Rather, the African dwarf-crocodile, *Osteolaemus tetraspis* Cope, will be reported below, and with significant emphasis on its possible two C.I.T.E.S. regulated subspecies.

Research on the African dwarf-crocodile by the Zoer 2006-2007 expedition (n=68 *Osteolaemus*) was conducted in the interior of Congo-Brazzaville (the Ubangi River drainage), the Kinshasa region in the western interior of Zaïre-DRC, and the Atlantic coastal zone of Congo-Brazzaville, Gabon, Cameroon, and Benin. The results about individual characters (different kinds of scale-counts) are presented and analysed locality by locality, in tables with similar formats, and often restricted to a single nation at a time, reflecting the listing of many whole nations in the written distributions of the two C.I.T.E.S. subspecies. All COAST localities are defined as *Osteolaemus tetraspis tetraspis* Cope, while the two INTERIOR localities are defined as the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies.

In order to compare specimens from two theoretically different ecologies, a primary distinction was made between African dwarf-crocodiles from along the equatorial Atlantic Ocean coast (mostly as whole nations), as opposed to animals from the equatorial interior of western Africa (the Ubangi River and the Ituri Forest) including Kinshasa. This ecological division is from existing literature, and is being tested in this thesis. For analysis, specimens from coastal countries will often be lumped together, and the same will happen for crocodiles from the more inland and central interior of Africa. Thus, Congo-Brazzaville (the equatorial Atlantic coast part of the nation), Gabon, Cameroon and Benin all got the label (place indication) “COAST” meaning *Osteolaemus tetraspis tetraspis*, while Congo-B (the Ubangi River region) and Zaïre-DRC got the label “INTERIOR” meaning *Osteolaemus tetraspis osborni*. The categories COAST and INTERIOR reflect definitions by C.I.T.E.S. The river drainage system is presented in Figure 1.3.

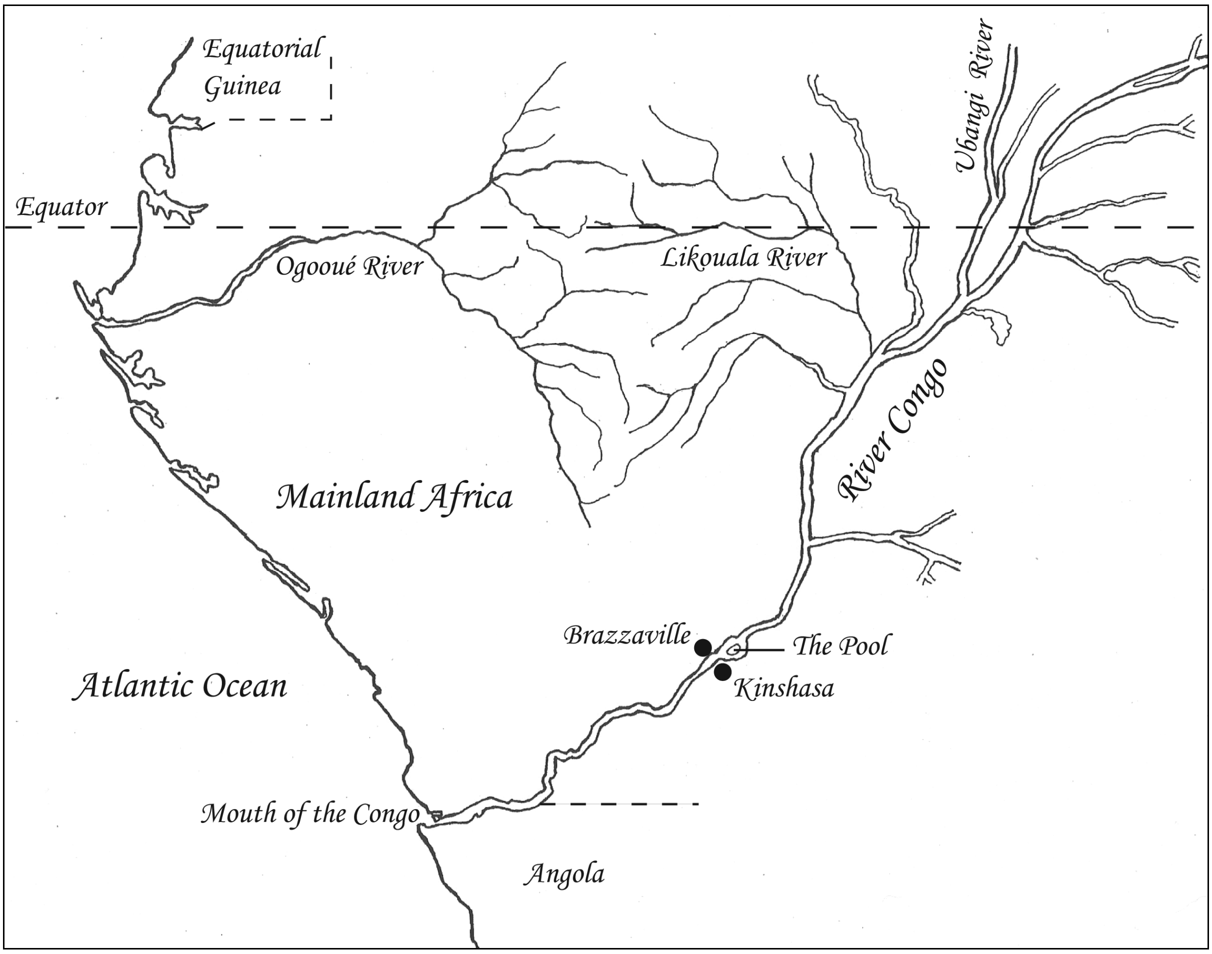


Figure 1.3 The river drainage systems in the researched countries

The relevant geographic division between *O. t. tetraspis* (type locality the Ogowe (Ogooué) River in Gabon) and *O. t. osborni* (type locality in the Ubangi River drainage) is the Ogowe-Likouala rivershed divide. The Likouala River is a tributary of the Ubangi, which in turn is a tributary of the Congo River upstream from the cities of Kinshasa and Brazzaville. The whole Ubangi drainage and also the Congo River as far downstream as Kinshasa is defined as INTERIOR, and everything else (theoretically from Cabinda to Senegal) is COAST.

1.6 IN *OSTEOLAEMUS*, GENERAL PATTERNS OF DIFFERENCES IN ANY DORSAL OR VENTRAL SCALE-COUNT CHARACTER'S RESULT MIGHT BE CAUSED BY GEOGRAPHIC VARIATION, OR POSSIBLY BY SEX

The external epidermal scales of the African dwarf-crocodile are the subject of most of the chapters of this thesis. The selected dorsal scale characters reported below are: the post-occipitals on the neck in Chapter 2, followed by the nuchals in Chapter 3. Later, the dorsal-armour division level between the body and the tail is established in Chapter 5, followed by the number of double-crested caudals in Chapter 6, and then the number of precaudal rows (between the tail and the neck) in Chapter 7. Lastly, the ratio between the numbers of double-crested caudal rows, compared with the numbers of precaudal rows, are combined together and then tried as a new available character in Chapter 8.

The two C.I.T.E.S. external ventral scalation characters, the collar-vent count and the transverse scale-count across the widest part of the belly, are presented and analysed together in Chapter 4 of this thesis. The general sizes of the dorsal and ventral scale-count samples are summarized and compared, and also the percentages of *Osteolaemus* specimens from (or for) which sex data was obtained is indicated in Table 1.4 (below).

Table 1.4 Comparative geographic frequency of *Osteolaemus* dorsal scales results, ventral scales results, and data about the animal's sex reported in this 2006-2007 sample

Locality + subspecies	dorsals + % with sex	ventrals + % with sex
A) *O. t. tetraspis*	n = 1 + 0,0 %	n = 0 + 0,0 %
B) *O. t. tetraspis*	n = 33 + 48,5 %	n = 30 + 53,3 %
C) *O. t. tetraspis*	n = 8 + 87,5 %	n = 8 + 87,5 %
D) *O. t. tetraspis*	n = 11 + 63,6 %	n = 6 + 100,0 %
E) *O. t. osborni*	n = 14 + 64,3 %	n = 2 + 100,0 %
F) *O. t. osborni*	n = 1 + 100,0 %	n = 1 + 100,0 %

Locality A = Benin nation represented by a single specimen from one local place (Porto Novo). Locality B = Cameroon represented collectively by four local places (Yaoundé, Campo Maan, Limbe, and Mundemba). Locality C = Gabon represented collectively by three local places (Setté Cama, Kango, and Gamba). Locality D = the Atlantic coastal part of Congo-Brazzaville nation represented collectively by four local places (Pointe-Noire, Bellelo, Youbi, and Dembouanou). Locality E = the interior part of Congo-Brazzaville represented by one local place (Likouala River drainage). Locality F = Zaïre-DRC at Kinshasa.

The six major localities (with 13 local places in total) that were mentioned above in Table 1.4, including the number of researched animals of a certain locality, are now plotted in Figure 1.4 (below).

<u>**Figure 1.4 Number of *Osteolaemus* researched at the different localities**</u>

The 68 African dwarf-crocodiles researched in the 2006-2007 expedition are plotted on this map. The concentration of researched animals is indicated by using different sizes of dots and by mentioning the actual number of specimens at the localities. In a comparison between this figure and Figure 1.3 (river drainage systems), both sides of the taxonomic boundary between the supposed two subspecies of African dwarf-crocodiles becomes clear. The localities of Likouala and Kinshasa (INTERIOR) represent *O. t. osborni*, and the other localities at the COAST represent *O. t. tetraspis*.

The animal's sex was not recorded on 28 *Osteolaemus*, out of a possible 68, for various accessibility reasons (essentially random), none of which should make these results invalid, except that in total they significantly decreased the size of the sample. The sex data about geographic groups in the 2006-2007 Zoer expedition's *Osteolaemus* sample is presented in Table 1.5 (below).

Table 1.5 Introductory geographic distribution of sex data about African dwarf-crocodiles presented with COAST and INTERIOR indications meaning the two C.I.T.E.S. kinds

Country	male	female	no data	total
Benin COAST	0	0	1	1
Gabon COAST	3	4	1	8
Cameroon COAST	8	8	17	33
Congo-B COAST	5	2	4	11
Congo-B INTERIOR	6	3	5	14
Zaïre-DRC INTERIOR	0	1	0	1
Total	**22**	**18**	**28**	**68**

In this table COAST means the *Osteolaemus tetraspis tetraspis* subspecies, and INTERIOR means the *Osteolaemus tetraspis osborni* subspecies. Sex data was obtained at three of the COAST general geographic localities, and also at two INTERIOR localities. When known, the sex ratio in this list of compared geographic places is relatively evenly balanced between males and females. Therefore, it is assumed that the ratio of male and female *Osteolaemus* in the no-data category is also in balance as roughly one to one.

Although incomplete, the data about the sex of the sample (n=68) of African dwarf-crocodiles, *Osteolaemus tetraspis* Cope, will be tested in Chapters 2-8 (below) as an available explanation for any significant trends in scale-count results that occur. The reason that the animal's sex remains unknown in many cases is that often it was possible to see the dorsal scalation, but it was not possible to obtain permission to turn the animal over, and further to manually probe its cloacal opening to determine the specimen's sex. Similarly, it was sometimes impossible to examine the ventral scalation, and also the taking of some other additional protocol characters, including the total stretched-out maximum length of the animal, were prohibited by circumstances including the wishes of the owners of the crocodiles.

Chapters 2-8 thus examine the *Osteolaemus* dorsal and ventral scalation data with regard to the place where the African dwarf-crocodile originated, and also secondarily with regard to the sex of the animal. In contrast to geography and gender, the total length of the crocodile is not expected to have any causal relation with any of the scalation characters in this thesis. The length of the African dwarf-crocodile does not influence the results of the dorsal and ventral scale-counts, because the scalation of crocodiles is already present in juveniles, and remains unchanged over the years.

There are two exceptions to the general rule of no ontogenetic change. First, the number of single-crest caudals decreases due to injury and wear on the tail. Counts of this character are thus possible only on undamaged individuals. So, the tip of the tail gets shorter throughout the crocodile's life as it gets "eroded" (= worn away) or damaged by competitors. Second, and more interesting, the number of scutes per dorsal transverse row in gharials (the species *Gavialis gangeticus* of India) decreases from six to four as an animal ages (Ross + Mayer 1983:313). Although length in general does not influence scale-count results in general, the range of length variation within this sample of African dwarf-crocodiles is presented in Table 1.6 (below).

Table 1.6 Extreme limits of total-length variation observed in the 2006-2007 sample of *Osteolaemus*

Country	shortest animal	longest animal	average length
Benin COAST	no data	no data	no data
Gabon COAST	20,50 cm	148,40 cm	90,54 cm
Cameroon COAST	28,0 cm	163,15 cm	80,79 cm
Congo-B COAST	28,0 cm	68,50 cm	47,23 cm
Congo-B INTERIOR	113,0 cm	156,50 cm	133,29 cm
Zaïre-DRC INTERIOR	143,60 cm	143,60 cm	143,60 cm

The longest of the *Osteolaemus tetraspis* in the 2006-2007 sample is a real indication of the total-length potential in African dwarf-crocodiles. However, and in contrast, the smallest total-length recorded by the Zoer expedition for *Osteolaemus* is not a lower limit size in this crocodile species, because all of the 2006-2007 expedition's animals of extremely small size had already hatched and dispersed into forest pools. Thus, no embryos emerging from the egg were measured, and it is assumed that African dwarf-crocodiles can be shorter than the 20,5 centimeter observed minimum (shown above).

The total-length question in the expedition's protocol involved measuring the animal two times. First, the length was measured above the resting and physically straightened-out crocodile. Second, the length was measured below the crocodile on a flat surface. Then, the average of the two results was arithmetically calculated to produce a general total-length number. These general (individually averaged) total lengths are divided into four categories of animal size in Table 1.7 (below).

Table 1.7 Geographic frequency of four wildlife size categories in this thesis sample of *Osteolaemus*

Country	0-50 cm	50-100 cm	100-150 cm	> 150 cm
Benin COAST	0	0	0	0
Gabon COAST	1	4	3	0
Cameroon COAST	9	8	8	3
Congo-B COAST	3	3	0	0
Congo-B INTERIOR	0	0	11	1
Zaïre-DRC INTERIOR	0	0	1	0

Because African dwarf-crocodiles longer than 150 centimeters in total length were measured in some COAST and also some INTERIOR localities, it is assumed that both of the two subspecies can attain similar maximum sizes.

Each crocodilian examined by the 2006-2007 expedition received a catalogue number in a series that was prefixed XXL. The individual longest *Osteolaemus* reported in this thesis is XXL-173 from Cameroon at Yaoundé (general length 163,15 cm). The second longest was XXL-111 from Congo-Brazzaville at the Likouala River (general length 156,50 cm). The third longest was XXL-130 from Gabon at Kango (general length 148,40 cm). Many of the tables in Chapters 2-8 will include XXL individual specimen numbers.

CHAPTER II POST-OCCIPITAL NECK-SCALES ARE TRANSVERSE ROWS INTERRUPTED ACROSS MIDLINE

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

2.1 INTRODUCTION

The question that is asked in this thesis is: “what African dwarf-crocodile scale-counts best support C.I.T.E.S. recognition of *Osteolaemus tetraspis osborni* (K.P. Schmidt)?” In other words, which, if any, scalation character on the African dwarf-crocodile justifies the current C.I.T.E.S. conclusion that two subspecies can be identified by scale-counts? In the search for what single character or combination of characters supports C.I.T.E.S. the best, the post-occipitals will be reviewed first in this thesis. Thus, here in Chapter 2, the question will be asked: do post-occipitals on the neck, nearest to the head, work as a 100% reliable method in the taxonomic recognition of specimens?

The Zoer expedition visited numerous countries on the African continent to collect as much information as possible on various different taxonomic characters of the living crocodiles. In this chapter the results of the character “post-occipitals” are presented country by country. Research on the African dwarf-crocodile in the 2006-2007 expedition was conducted in the interior of Congo-Brazzaville (the Ubangi River drainage part), the Kinshasa region in the interior of Zaïre-DRC, and also the coastal zone of Congo-Brazzaville, Gabon, Cameroon and Benin. Data about individual characters are presented by nation of origin in tables with a similar style of format. This format is used in every chapter of this thesis where a taxonomic character is discussed.

As mentioned in Chapter 1 a comparison is made between specimens from the equatorial Atlantic coast nations, as compared with animals from far inland in central Africa. In this case, Cameroon, Gabon and Congo-Brazzaville (equatorial Atlantic coast) all got the label (place indication) “COAST” (meaning *O. t. tetraspis*), while in contrast, Congo-Brazzaville (Ubangi River region) and Zaïre-DRC got the label “INTERIOR” (meaning *O. t. osborni)*.

According to the ecological notes by Herbert Lang, in Schmidt (1919:432), the dwarf-crocodile population in the Ituri Forest and the Ubangi River region of central Africa is remarkably similar in external appearance to the *Osteolaemus tetraspis* Cope population along the equatorial Atlantic Ocean coast of the continent. Thus, in the estimation of the original collector of the Ubangi drainage type-specimen and two paratype specimens (and also the Congo River individual from near Stanley Falls that got lost) of *Osteoblepharon osborni* Schmidt, the two kinds of African dwarf-crocodiles looked the same, until after the internal anatomy of their noses was examined in New York City.

If the nasal anatomy of *Osteoblepharon* Schmidt, 1919, had not appeared to K.P. Schmidt as significantly different from the completely ossified septum dividing the external nostrils from each other in the genus *Osteolaemus* Cope, 1861, then there would have been no reason to name the Ubangi River and middle and upper Congo River (Stanley pool and upstream to and beyond Stanley Falls = Kinshasa to Kisangani and beyond) population as a species (or subspecies). The American Museum of Natural History's 1909-1915 famous Congo Expedition would have merely established a range-extension for E.D. Cope's genus and species from 1861.

The cotype skull of *Osteolaemus tetraspis* Cope was a single individual (without detailed locality data), and the earliest picture of the bony nasal-septum in *Osteolaemus tetraspis* Cope was an adult skull from the Atlantic Ocean coast of Nigeria (at “Old Calabar”) published by John Edward Gray (1867). There also existed an earlier excellent plate of a juvenile African dwarf-crocodile from “Old Calabar” in Andrew Murray's (1862) type description of *Crocodilus frontatus* Murray, and this picture showed the scales on the tail and the body and neck, including the post-occipitals, the group of dorsal armour scales that is immediately posterior to the crocodile's head.

2.2 METHODS

All neck-shields and post-occipital scales of the specimens examined by the 2006-2007 sample were recorded on a field-protocol. The post-occipital scales were divided into two transverse rows. Then, the number of scales in the anterior and posterior row, and also the number of scales to the left and to the right of the dorsal long-axis midline were recorded. The theoretical or ancestral transverse rows of post-occipitals (PO's) always have the left and right halves in each transverse row separated from each other by a space of flexible and unarmoured skin covering the dorsal long-axis midline. In addition to answering the protocol questions, supplementary drawings were sometimes made by hand, and photographs were often taken of the neck of the crocodile. The position of the post-occipitals (PO's) is indicated in Figure 2.1, below.

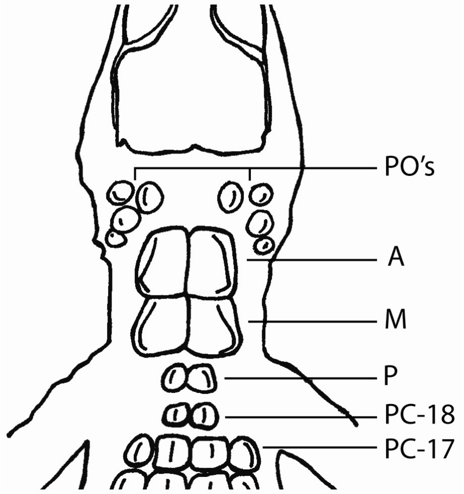


Figure 2.1   The post-occipitals on the neck

This male (XXL-124) from the rainforest near Youbi (Congo-Brazzaville, COAST) shows the post-occipitals (PO's) of a dwarf-crocodile, which are present in two transverse rows of four each. The post-occipitals are symmetrically arranged across the dorsal midline. In addition, posterior to the post-occipitals, the anterior row (A) of the big neck-shields ("nuchals"), the middle pair of nuchal scales (M), and the posterior optional shortest row of nuchals (P) are indicated as well. These special neck-shields of the African dwarf-crocodile, that are called the nuchals, will be discussed in Chapter 3 of this thesis. Additionally, at the bottom, the figure shows the anteriormost precaudal rows (PC-17 and PC-18) in the thoracic region. The "PC" (precaudal) numbering system for transverse rows on the body (and also the tail in a similar system) will be explained in Chapter 7 (and Chapter 6), below.

2.3 RESULTS

According to Peter Brazaitis (1973:79), the African dwarf-crocodiles from the interior of Congo-Brazzaville and the Kinshasa region (*Osteolaemus tetraspis osborni*) usually have two transverse rows of post-occipital scales, as compared with coastal specimens (*Osteolaemus tetraspis tetraspis*) which usually have only a single transverse row of post-occipital scales. An original assertion in Schmidt (1919:424) about the number of transverse rows of post-occipitals in dwarf-crocodiles from Africa was more clearly written by Brazaitis (1973), and will be tested by evidence in this 2006-2007 sample from the Ubangi River drainage in the interior of Congo-Brazzaville, the Kinshasa region in the interior of Zaïre-DRC, the coastal zone of Congo-Brazzaville, Gabon, Cameroon and Benin. The data results about the post-occipitals from these localities are introduced in Table 2.1, below. Additional results concerning geography and sex will be detailed in several tables in this chapter (below). In essence, the Brazaitis (1973:79) characterizations were: "post-occipitals: usually a single transverse row of sharply raised scales" = COAST, compared with "post-occipitals: 2 transverse rows of 4 scales, separated from each other" = INTERIOR. Note that the individual in Figure 2.1 (above) has two transverse rows of 4 scales, not especially separated from each other, and thus this individual COAST animal (XXL-124) keys to INTERIOR by Brazaitis (1973) post-occipitals.

Table 2.1 Summary of answers to four protocol questions about the post-occipitals

Questions about the necks on dwarf-crocodiles	yes, in how many
Post-occipitals (PO's) on the neck are recorded?	57
No results on the post-occipitals (PO's) on the neck?	11 (A)
Post-occipitals (PO's) are present in two transverse rows?	32
Absence of a second transverse row of PO's?	25 (B)

In a total of 68 *Osteolaemus tetraspis* Cope specimens studied, on only 57 African dwarf-crocodiles the post-occipitals were recorded. The majority of the eleven animals (A), without data on the post-occipitals, were found in local bushmeat markets or on the side of the road (XXL-104, #105, #126 and XXL-127 Congo-Brazzaville at Pointe-Noire COAST; and XXL-#136 Gabon at Setté Cama COAST; and XXL-164 Cameroon at Campo Maan COAST; and XXL-166, #172 and XXL-174 Cameroon at Yaoundé COAST; and lastly XXL-180 and XXL-181 Cameroon at Limbe COAST). Twenty-five animals (B) had only one transverse row of post-occipitals. However, the majority of the *Osteolaemus* encountered by the 2006-2007 expedition had the post-occipitals in two transverse rows.

In this 2006-2007 sample, African dwarf-crocodiles can have their post-occipitals in one, or alternatively in two transverse rows. The 57 specimens on which the post-occipitals have been recorded, will have their appearances further discussed in this chapter.

2.3.1 Post-occipitals in one or two transverse rows

The 32 African dwarf-crocodiles with their post-occipitals in two transverse rows, including their locality details and geographic-kind of subspecies, are displayed and analysed in Table 2.2, below. The other 25 specimens with post-occipitals in just one transverse row will be presented separately (below).

Table 2.2 Specimens with post-occipitals (PO's) in two transverse rows

Locality detail and geographic-kind	frequency in locality (n=57)
Porto Novo = COAST subspecies	1 out of 1 in Benin nation
Yaoundé = COAST subspecies	7 out of 27 in Cameroon
Mundemba = COAST subspecies	1 out of 27 in Cameroon
Campo Maan = COAST subspecies	4 out of 27 in Cameroon
Fifteen animals from Cameroon have one transverse row of PO's (Table 2.3, below)	
Gamba = COAST subspecies	1 out of 7 in Gabon nation
Six animals from Gabon have one transverse row of PO's (below)	
Locality detail and geographic-kind	frequency in locality (n=57)
Pointe-Noire = COAST subspecies	1 out of 7 in coastal-Congo
Youbi = COAST subspecies	1 out of 7 in coastal-Congo
Bellelo = COAST subspecies	2 out of 7 in coastal-Congo
Three animals from coastal Congo (Brazzaville) are different (below)	
Likouala = INTERIOR subspecies	13 out of 14 in interior-Congo
One animal from interior Congo (Brazzaville) is different (below)	
Kinshasa = INTERIOR subspecies	1 out of 1 in Zaïre-DRC

All six localities, thus including both "COAST" and "INTERIOR", are present in this table of 32 out of 57 total animals. All COAST localities are *Osteolaemus tetraspis tetraspis* Cope, while the two INTERIOR locations are the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies. The 100% sample from Benin is just one animal, while in contrast and much more significantly, the thirteen out of fourteen animals from the interior of Congo-Brazzaville, which have their post-occipitals in two transverse rows, is a strong majority. The other interior locality (Zaïre-DRC) is also present in the category with two transverse rows in 100% of a sample of one.

Although it can be notoriously difficult to make generalizations about the post-occipital scales on any crocodilian, the African dwarf-crocodiles in this sample of 32 (out of 57) confirms that both COAST animals and INTERIOR animals can have their post-occipitals arranged in two transverse rows. The 2006-2007 field-collected *Osteolaemus* sample (57 with PO data) is probably large enough to draw the conclusion that post-occipitals in two rows is actually not a very highly predictive character for the recognition of *Osteolaemus tetraspis osborni*, K.P. Schmidt.

The herpetologist Karl Patterson Schmidt (1919:424) said that dwarf-crocodiles from the “INTERIOR” locations (*Osteolaemus tetraspis osborni*, K.P. Schmidt) always have two transverse rows of post-occipitals with four scales in each, with the anterior being the larger row, and in all rows with each scale separate and prominently keeled. However, some of the Zoer expedition specimens show a different pattern. Note that in contrast, Schmidt (1919) suggested that *Osteolaemus tetraspis tetraspis* (the other subspecies) has two transverse rows of post-occipitals of two scales each, but this assertion about the COAST was merely a picture of one animal, lacking precise locality information.

Before testing the sex-variation hypothesis as another possible way of correlating the post-occipital scale character with biology, first the dwarf-crocodiles from the 2006-2007 sample with just one transverse row of post-occipitals on the neck are presented in Table 2.3, below.

Table 2.3 One transverse row of post-occipitals present

Locality detail and geographic-kind	frequency in locality (n=57)
Yaoundé = COAST subspecies	10 out of 27 in Cameroon
Mundemba = COAST subspecies	1 out of 27 in Cameroon
Campo Maan = COAST subspecies	4 out of 27 in Cameroon
--- --- --- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- ---
Setté Cama = COAST subspecies	4 out of 7 in Gabon nation
Kango = COAST subspecies	2 out of 7 in Gabon nation
--- --- --- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- ---
Locality detail and geographic-kind	frequency in locality (n=57)
Bellelo = COAST subspecies	2 out of 7 in coastal-Congo
Dembouanou = COAST subspecies	1 out of 7 in coastal-Congo
--- --- --- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- ---
Likouala = INTERIOR subspecies	1 out of 14 in interior-Congo

Only a minority (25 out of 57) of the African dwarf-crocodiles from this 2006-2007 sample have their post-occipitals arranged in one transverse row. However, out of these 25 specimens, only one INTERIOR animal had only one transverse row of post-occipital scales, which suggests a significant minority (n=15 INTERIOR total).

African dwarf-crocodiles from the equatorial Atlantic coastal region and also from the inland interior of the continent can have their post-occipitals in one transverse row, or alternatively in two transverse rows. Therefore, because both conditions occur in both “COAST” and “INTERIOR” localities, the post-occipitals as two transverse rows, or alternatively one row, is not a totally reliable character for the recognition of (sub)species.

The sex-variation hypothesis in Table 2.4 (below) is another possibility for correlating the post-occipital scales with biology. Seven out of 11 African dwarf-crocodiles excluded from the PO sample were without sex-data (XXL-104, #105, #126, and XXL-127 Congo-Brazzaville at Pointe-Noire COAST; and XXL-164 Cameroon at Campo Maan COAST; and XXL-180, and XXL-181 Cameroon at Limbe COAST. Three females (XXL-166, #172, and XXL-174) without sex-data were from Cameroon at Yaoundé COAST; and one male (XXL-136) was from Gabon at Setté Cama COAST.

Table 2.4 Transverse rows of post-occipitals sex-data examined

Locality and subspecies	rows of PO's	frequency and country	sex
Porto Novo = COAST (#185)	2 trans. rows	1 out of 1 from Benin	no
Kango & Setté Cama = COAST	1 trans. row	6 out of 7 from Gabon	A
Gamba = COAST (#139)	2 trans. rows	1 out of 7 from Gabon	no
Mundemba, Yaoundé, and Campo Maan = COAST	1 trans. row	15 out of 27 Cameroon	B
Mundemba, Yaoundé, and Campo Maan = COAST	2 trans. rows	12 out of 27 Cameroon	C
--- --- --- --- --- ---	--- --- ---	--- --- --- --- ---	---
Locality and subspecies	rows of PO's	frequency and country	sex
Bellelo & Dembouanou = COAST	1 trans. row	3 out of 7 Congo-B	D
Bellelo, Pointe-Noire, and Youbi = COAST	2 trans. rows	4 out of 7 Congo-B	E
--- --- --- --- --- ---	--- --- ---	--- --- --- --- ---	---
Likouala = INTERIOR (#118)	1 trans. row	1 out of 14 Congo-B	male
Likouala = INTERIOR	2 trans. rows	13 out of 14 Congo-B	F
Kinshasa = INTERIOR (#17)	2 trans. rows	1 out of 1 Zaïre-DRC	female

A = XXL-130 female, #132 male, #s 134-135 females, #137 male, #138 female; and B = #s 150-153, 156-157, and 159 all with no-sex, 160 male, 169-170 male, 171 female, 175 female, 176 no-sex, 182 female, 183 male; and C = #148-149 no-sex, 154-155 no-sex, 158 no-sex, 161 female, 162 male, 163 no-sex, 165 male, 167 female, 173 male, 184 male; and D = XXL-107 female, 109 male, 125 male; and E = XXL-106 female, #108 male, 124 male, 128 male; and F = #110-111 males, 112 female, #s 113-117 no-sex, 119-121 males, 122-123 females. The data in Table 2.4 appears to be random about which sex has one or two transverse rows of post-occipitals. Three of the four samples where one is 100% of one in this table cancel each other out, being one male, one female and one with no data. One additional specimen with no data about sex remains. A = 6 with sex data from Gabon (2 males, 4 females). B = 7 with sex from Cameroon (4 males, 3 females). C = 6 more additional Cameroon with sex (4 males, 2 females). D = 3 more Cameroon with sex data (2 males, 1 female). E = 4 with sex from Congo-Brazzaville coast (3 males, 1 female). F = 8 with sex data from Congo-Brazzaville interior (5 males, 3 females).

While making the transition from *Osteolaemus* with one symmetrical row of PO's, to those African dwarf-crocodiles with two symmetrical rows of post-occipitals, it is noteworthy that some of the sample included some bilateral asymmetry in the PO region, and these asymmetrical cases will be discussed below, later. Also, as a theoretical consideration, it is possible that the two transverse rows that are reported in this chapter are a wrong interpretation. For example, the post-occipital scales on XXL-124 in Figure 2.1 (above) could be interpreted as an anterior transverse row of four PO's, and then a middle row of two scales, followed by a third transverse row (very broadly interrupted across the midline region) of PO's with two scales in it. This three row interpretation is possibly good biology, but is ignored in this thesis, because C.I.T.E.S. interprets the post-occipital scales in Figure 2.1 as two transverse rows of four scales each. This also is not necessarily true biology, but the two row model is here applied, because it is a C.I.T.E.S. hypothesis about subspecies that is being tested.

2.3.2 Arrangement patterns of PO's with two transverse rows

In Table 2.4 (above) all specimens on which the post-occipitals got recorded in the 2006-2007 field-collected *Osteolaemus* sample were presented, including notes about data about the sex of the animals. Sex does not seem to explain the observed variation in PO scales, because both sexes occur in coastal areas, and also both sexes occur in the inland localities, and both were found to have either one or two transverse row(s) of post-occipitals. However, the African dwarf-crocodiles with their post-occipitals in two transverse rows can have different numbers of scales in their individual rows. In this sample three manifestations of PO's in two transverse rows occur the most frequently. Other than these three manifestations, a few additional specimens were encountered with other arrangements of PO's, arranged both symmetrically and asymmetrically. The frequency of each manifestation is presented in Table 2.5, below.

Table 2.5 Number of PO's in case of two transverse rows

Arrangement of post-occipital scales	frequency
Two transverse rows of four each	6 out of 32
Four in anterior row, two in posterior row	18 out of 32
Two in anterior row, four in posterior row	4 out of 32
Other arrangements of PO's in two rows	4 out of 32

The majority of the specimens with two transverse rows of post-occipitals have four PO's in the anterior row, and two in the posterior row, arranged in a symmetrical pattern. Additionally, there are two other conditions which occur less frequently (two transverse rows of four each, and two in the anterior row and four in the posterior row). The post-occipitals are symmetrically arranged across the dorsal long-axis midline in all three possibilities mentioned above. The four other arrangement patterns of PO's will be discussed in Table 2.12, below.

The first "other" pattern of PO's in dwarf-crocodiles to be discussed is the one with their post-occipitals arranged in two transverse rows of four scales each. These specimens are presented, and their sex-data is examined for possible correlations, in Table 2.6, below.

Table 2.6 Two transverse rows of four PO scales each

Locality detail and geographic-kind	frequency in locality (n=57)	sex
Yaoundé = COAST subspecies	1 out of 27 in Cameroon	no
Gamba = COAST subspecies	1 out of 7 in Gabon	no
Locality detail and geographic-kind	frequency in locality (n=57)	sex
Youbi = COAST subspecies	1 out of 7 in coastal-Congo	male
Likouala = INTERIOR subspecies	2 out of 14 in interior-Congo	both female
Kinshasa = INTERIOR subspecies	1 out of 1 in Zaïre-DRC	female

Six African dwarf-crocodiles from the Zoer 2006-2007 sample have their post-occipitals in two transverse rows of four scales each. These post-occipitals are symmetrically arranged across the dorsal long-axis midline. Animals with coastal ecology as well as animals from the inland are evenly represented in this table, and both sexes can exhibit this character, but the sample is probably too small to draw any reliable conclusions, except that the condition can be expected to occur in any large sample.

The occurrence rate of post-occipitals in two rows of four scales each is very low in the Zoer 2006-2007 sample of 57 African dwarf-crocodiles. However, the probability of a specimen having its post-occipitals in two transverse rows, with four scales in the anterior row, and two scales in the posterior row, is high. These specimens and their sex-data are presented and examined in Table 2.7, below.

Table 2.7 Four PO scales in anterior row, two in posterior row

Locality detail and geographic-kind	frequency in locality (n=57)	sex
Porto Novo = COAST subspecies	1 out of 1 in Benin	no
--- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- --- ---	---
Yaoundé = COAST subspecies	3 out of 27 in Cameroon	A
Campo Maan = COAST subspecies	4 out of 27 in Cameroon	B
--- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- --- ---	---
Locality detail and geographic-kind	frequency in locality (n=57)	sex
Pointe-Noire = COAST subspecies	1 out of 7 in coastal-Congo	male
--- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- --- ---	---
Likouala = INTERIOR subspecies	9 out of 14 in interior-Congo	C

Eighteen African dwarf-crocodiles from the Zoer 2006-2007 sample of 57 have their post-occipitals in two transverse rows, with four scales in the anterior row, and two scales in the posterior row: A = XXL-155 with no sex, #167 female, and #173 male; B = XXL-161 female, #162 male, #163 with no sex, and XXL-165 male; C = XXL-#s 110-111 males, #112 female, #113, 114, and 117 all with no sex, #119 , 120, and 121 males. The post-occipitals are symmetrically arranged across the dorsal long-axis midline. The two single animals in Table 2.7 are one male and one with no data. A = 2 with sex from Cameroon (1 male, 1 female); B = 3 more Cameroon with sex (2 males, 1 female); and C = 6 with sex from Congo-Brazzaville interior (5 males, 1 female).

Again, there is no observable correlation between this special post-occipital scale character and either sex or locality, because the animals from both COAST and INTERIOR localities are both male and female. The third arrangement pattern of bilaterally symmetrical post-occipitals is animals with their post-occipitals in two transverse rows as detailed in Table 2.8, below. These four animals have two PO's in the anterior row, and have four PO's in the posterior row.

Table 2.8 Two PO scales in anterior row, four in posterior row

Locality detail and geographic-kind	frequency in locality (n=57)	sex
Yaoundé = COAST subspecies	2 out of 27 in Cameroon	no
Mundemba = COAST subspecies	1 out of 27 in Cameroon	male
--- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- --- ---	---
Locality detail and geographic-kind	frequency in locality (n=57)	sex
Likouala = INTERIOR subspecies	1 out of 14 in interior-Congo	no

Only four animals in this sample have two scales in the anterior and four scales in the posterior row of post-occipitals, being one male, and three with no sex. The post-occipitals of these animals are symmetrically arranged to either side of the dorsal long-axis midline.

2.3.3 Arrangement patterns of PO's in cases of one transverse row

In the next three tables the African dwarf-crocodiles with just one transverse row of PO's will be discussed. In addition to the animals with their post-occipitals in two transverse rows, the Zoer 2006-2007 expedition also encountered twenty-five (25) animals with just one transverse row of post-occipitals. The frequency and nature of variations in single-row PO examples is presented in Table 2.9, below.

Table 2.9 Number of PO scales exhibiting only one transverse row

Arrangement of post-occipital scales	frequency
Four scales in single transverse row	21 out of 25
Two scales present in the only row	2 out of 25
Other kinds of single-row PO's	2 out of 25

The majority of the animals with a single transverse row of post-occipitals have four scales in it, and the scales are arranged bilaterally symmetrically. Two specimens have just two scales in the row, and they too are symmetrical in relation to the dorsal midline. Note that two additional animals show slightly different (and in these cases asymmetrical) patterns of post-occipitals with only the anterior row present, as will be shown later in Table 2.12, below.

In this n=25 sample, twenty-one specimens have four scales present in their single transverse row of post-occipitals. Localities represented in this 2006-2007 sample are Cameroon, Gabon, the Ubangi River drainage in the interior of Congo-Brazzaville, and also the coastal zone of Congo-Brazzaville. In all localities sampled, except for Benin, this formation of PO's was encountered. These animals are lumped together and their political locality, general ecology, and sex are examined for correlations in Table 2.10, below.

Table 2.10 Four scales in single transverse row, sex-data examined

Locality detail and geographic-kind	frequency in locality (n=57)	sex
Yaoundé = COAST subspecies	9 out of 27 in Cameroon	A
Mundemba = COAST subspecies	1 out of 27 in Cameroon	female
Campo Maan = COAST subspecies	2 out of 27 in Cameroon	B

--- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- ---

Setté Cama = COAST subspecies	4 out of 7 in Gabon nation	C
Kango = COAST subspecies	2 out of 7 in Gabon nation	D
--- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- ---	--- ---
Locality detail and geographic-kind	frequency in locality (n=57)	sex
Bellelo = COAST subspecies	1 out of 7 in coastal-Congo	female
Dembouanou = COAST subspecies	1 out of 7 in coastal-Congo	male
--- --- --- --- --- --- --- --- ---	--- --- --- --- --- --- ---	--- ---
Likouala = INTERIOR subspecies	1 out of 14 in interior-Congo	male

Twenty-one African dwarf-crocodiles from the Zoer 2006-2007 sample of 57 have their post-occipitals in one transverse row with four scales in it: A = XXL-#s150-153 with no sex, 156-157 with no sex, 169-170 males, and XXL-171 female; B = XXL-160 male, and #176 with no sex; C = XXL-#s 134-135 females, #137 male, and XXL-138 female; D = XXL-130 female, and XXL-132 male. The post-occipitals are symmetrically arranged across the dorsal long-axis midline. The four single animals in this table cancel each other out, being two males and two females. A = 3 with sex from Cameroon (2 males, 1 female); B = 1 more Cameroon with sex (male); C = 4 with sex from Gabon (1 male, 3 females); and D = 2 more with sex from Gabon (1 male, 1 female). The post-occipitals are symmetrically arranged across the dorsal long-axis midline in all twenty-one of these African dwarf-crocodiles. The influence of sex appears minimal, and both of the major ecological categories are represented.

The second symmetrical arrangement of PO's with only two scales in a single row is displayed in Table 2.11, below. These two African dwarf-crocodiles were encountered by the Zoer 2006-2007 Africa expedition at two different localities on the Atlantic coast of Cameroon.

Table 2.11 Two scales occupy the one transverse row present

Locality detail and geographic-kind	frequency in locality (n=57)	sex
Mundemba = COAST subspecies	1 out of 27 in Cameroon	male
Campo Maan = COAST subspecies	1 out of 27 in Cameroon	female

Two animals from Cameroon (from Mundemba, and at Campo Maan) have two scales present in their single transverse row. One is a male, and one is a female. The PO scales are again symmetrically arranged to either side of the dorsal long-axis midline on these two African dwarf-crocodiles.

Some animals with other additional patterns of post-occipitals (PO rows of scales) were encountered at Congo-Brazzaville coast, Congo-Brazzaville interior, and in Cameroon. These six animals, with one or two transverse rows, and with various (symmetrical and asymmetric) arrangements of PO's, are displayed in Table 2.12 (below).

Table 2.12 Six other manifestations of post-occipitals, symmetric and asymmetric

XXL# and sex	locality	anterior row	posterior row	(a)symmetric
#158, no-sex	Yaoundé	2 PO's (1/1)	2 PO's (1/1)	symmetrical
#159, no-sex	Yaoundé	3 PO's (2/1)	absent	asymmetric
--- --- --- --- ---	--- --- ---	--- --- ---	--- --- --- --- ---	--- --- ---
XXL# and sex	locality	anterior row	posterior row	(a)symmetric
#106, female	Bellelo	6 PO's (3/3)	2 PO's (1/1)	symmetrical
#108, male	Bellelo	4 PO's (2/2)	6 PO's (3/3)	symmetrical
#109, male	Bellelo	5 PO's (2/3)	absent	asymmetric
--- --- --- --- ---	--- --- ---	--- --- ---	--- --- --- --- ---	--- --- ---
#115, no-sex	Likouala	3 PO's (1/2)	2 PO's (1/1)	asymmetric

In Congo-Brazzaville on the coast (at Bellelo), and in Congo-Brazzaville in its interior (at Likouala), and also in Cameroon (at Yaoundé), six animals with other arrangement patterns of post-occipitals (PO's) were encountered. Some are symmetrically arranged, and some are asymmetrical in relation to the dorsal long-axis midline. Again, both the COAST and the INTERIOR exhibit essentially overlapping character states. This concludes the entire sample of fifty-seven (57) African dwarf-crocodiles with PO data.

As mentioned earlier it is often extremely difficult to characterize the post-occipital scales on any crocodilian in simple terms, and the African dwarf-crocodiles from this sample appear to confirm that generalization. The 2006-2007 sample of African dwarf-crocodiles at the different localities is large enough to draw the conclusion that variation in PO's is essentially random. This is true when analysed as two transverse rows, as it is done in the existing literature. It is possible that the two row model for PO's does not apply to the African dwarf-crocodile, but no matter how they are interpreted and counted, the post-occipitals appear to be randomly variable. The post-occipitals are not a 100% reliable character for the recognition of *Osteolaemus tetraspis osborni*, K.P. Schmidt. However, in Chapter 3 (below) the reliability of another crocodilian neck-scales character will be tested and discussed. Fortunately, the large scales located posterior to the post-occipitals, called "the nuchals", are generally more taxonomically useful on living crocodilians.

2.4 REVIEWING THE POST-OCCIPITAL SCALES

The Ross + Mayer (1983) paper did not interpret the post-occipital scales as necessarily being arranged in one or two transverse rows in this species. Rather, Ross + Mayer (1983:319) state that the dorsal part of the neck that is closest to the head is not yet understood in the African dwarf-crocodile, *Osteolaemus tetraspis*. However, the hypothesis from K.P. Schmidt (1919), and the hypothesis from P. Braziatis (1973), are both falsified by the Zoer expedition's sample of 57 examples of post-occipitals, because the two transverse rows of four scales that was predicted to characterize the INTERIOR (*Osteolaemus tetraspis osborni*) population can also occur in the COAST (*Osteolaemus tetraspis tetraspis*) animals, and to a lesser degree the predicted COAST condition can also occur in the INTERIOR. The sex of the African dwarf-crocodile appears to have little or no influence on the number and placement of its post-occipital scales, including the general presence of bilateral symmetry, or alternatively the infrequent absence of bilateral symmetry observed in this 2006-2007 sample.

CHAPTER III NUCHAL NECK-SCALES ARE TRANSVERSE ROWS CONTIGUOUS ACROSS MIDLINE

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

3.1 INTRODUCTION

If the post-occipital (PO) scales in Chapter 2 are really arranged in transverse rows, it is often difficult in practice to see it, and the theoretical or ancestral transverse rows of post-occipitals (PO's) always have the left and right halves in each transverse row separated from each other by a space of flexible and unarmoured skin covering the dorsal long-axis midline. Thus, in theory, the PO's in the anterior part of the neck, closest to the head, are easily distinguishable from the transverse rows of nuchal scales in the more posteriorly located cervical shield, because the left-side nuchals contact the right-side nuchals directly, creating a contiguous transverse series that crosses the dorsal long-axis midline.

The multi transverse-rowed neck-shields are a characteristic feature in crocodiles and need study, because of possible variation in shape and in number of transverse rows. According to Ross + Mayer (1983) (available in Annexure A) there are three transverse rows of nuchal scales in the cervical shield of the African dwarf-crocodile, *Osteolaemus tetraspis* Cope. These three rows occupy the space between the post-occipitals (PO's) and the anterior end of the thoracic body armour, and Ross + Mayer (1983:319) said that each of the three transverse rows has a maximum of two scales in it. Thus, the largest number of nuchal scales on one dwarf-crocodile is six, being three pairs of two. This African dwarf-crocodile scale-count will be tested for support of the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies.

However, Ross + Mayer (1983) also allowed the most posterior of the three transverse-rows to be diminished to one scale (a degenerative and vestigial condition), or to disappear (more or less) completely. Thus, the genus *Osteolaemus* Cope has two transverse rows of nuchals that are obligatory, and a third cervical-shield row that is optional (discussed below in Section 3.3.2).

In this chapter the results about "the nuchals" will be presented and analysed country by country. Research on the African dwarf-crocodile in the 2006-2007 expedition was conducted in the interior of Congo-Brazzaville (the Ubangi River drainage), the Kinshasa region in the interior of Zaïre-DRC, the coastal zone of Congo-Brazzaville, Gabon, Cameroon and Benin. The results about a certain character are presented by country in tables with a similar format. This format is used in every chapter of this thesis in which characters are being discussed.

Similarly, a comparison here is made between specimens from the equatorial Atlantic coastal nations, as compared with animals from far inland in central Africa. In this case, Cameroon, Gabon and Congo-Brazzaville (equatorial Atlantic coast) all got the label (place indication) “COAST” (meaning *O. t. tetraspis*), while in contrast, Congo-Brazzaville (Ubangi River region) and Zaïre-DRC got the label “INTERIOR” (meaning *O. t. osborni*).

3.2 METHODS

The different shields (scales) on the neck region of the African dwarf-crocodile were studied carefully, and the dorsal surface of the neck was cleaned when necessary. First of all, a series of six questions were systematically answered. These questions were present in the field-protocol, and were answered in a specific order.

The questions about the length and shape of the different transverse rows, and the possibility of skin in between rows of scales were:

- Is the anterior pair of scales longer than, equal to, or shorter than the middle pair of scales?
- Is the middle pair of scales longer than, equal to, or shorter than the anterior pair of scales?
- Is the posterior, optional, shortest row present? If so, does it have one or two scales in it?
- Is there skin in between the middle pair of scales and PC-19?
- Is there skin in between PC-19 and the thorax?
- Are the nuchals on the neck anomalous?

The protocol asked some questions more than one way, to make the results absolutely clear (example: Is the anterior row longer than the middle row? Is the middle row longer than the anterior row?). Sometimes it was not possible to determine the relation between the neck-shields with the naked eye. Sliding metric callipers (metal) were employed whenever there was any ambiguity. For example, sometimes the anterior and posterior obligate transverse-rows appeared to be the same length, but when measured (as maximums) a very small difference was found.

Apart from answering the questions from the field-protocol (above), drawings were made by hand and pictures were taken of the neck of the crocodile. In this way the answers to the questions from the field-protocol could be compared with the drawings and pictures to affirm the results. The area shown in Figure 3.1 (below) includes some continuous precaudal rows on the body, and then goes anterior along the length of the neck to the back edge of the cranial table, and the whole head.

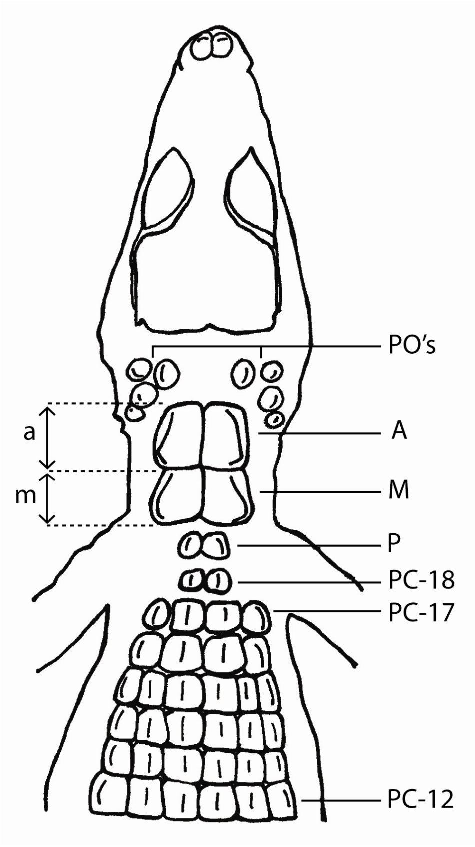


Figure 3.1 The neck-shields of the cervical zone

This male African dwarf-crocodile (XXL-124) from the rain forest near Youbi (Congo-Brazzaville) shows the studied neck area. The twelfth continuous precaudal row (PC-12) on the body was marked with coloured tape as part of the examination procedure. The anteriormost continuous precaudal row on the body is PC-17. The anterior pair of scales (A), the middle pair of scales (M) and the posterior optional row (P) are the three rows of the cervical-shield. The arrows (on the left) show how the length of the anterior (a) and middle (m) pair of scales was measured.

Because of the fact that the nuchal scales are more obvious than the PO's, the number of African dwarf-crocodiles in the 2006-2007 sample with information about these large "nuchal" neck scales is slightly higher. There were only 57 PO's, but there will be 68 nuchals. The next section starts with an introduction to the sometimes remarkably surprising results about this "nuchals" character.

3.3 RESULTS

The probable function of the nuchal scales, and their arrangement into a cervical shield, is the protection of the neck-muscles underneath them, and almost all 68 of the African dwarf-crocodiles examined by the Zoer *Osteolaemus* expedition had their dorsal midline cervical-muscles uniformly protected by their cervical shields. Each animal had an equal amount of bone covering the same basic place on its neck (except a very few which exhibited severely eroded and worn-down nuchals). Sometimes the nuchal scales achieved unexpected combinations involving the uniting of ordinarily separate pieces of bone. Two significant assertions in Ross + Mayer (1983:319) about the two obligate rows of the cervical shield in dwarf-crocodiles from Africa were falsified (shown to be inadequate) by evidence in this 2006-2007 sample from Benin, Cameroon, Gabon, the Ubangi River drainage in the interior of Congo-Brazzaville, the Kinshasa region in the interior of Zaïre-DRC, and the coastal zone of Congo-Brazzaville, all lumped together in Table 3.1 without concern about geography or sex (to be detailed below in this chapter).

Table 3.1 Unexpected part of the nuchal-scales data (n=68) classified as "other" and postponed for specialist's study

Questions about the necks on dwarf-crocodiles	yes, in how many
Anterior two nuchal rows okay for length comparison?	61
Anterior two nuchal rows not okay for length comparison?	7
All obligate nuchal rows are pairs of two scales?	57
Some obligate nuchal rows are not a pair of scales?	4

Out of a possible 68 *Osteolaemus tetraspis* Cope, only 61 African dwarf-crocodile neck-shields were suitable for analysis using the Ross + Mayer (1983) model. This is a surprising result, because only one specimen (XXL-130) was damaged, while six others (XXL-115, #139, #153, #156, #157 and XXL-181) exhibited entirely unexpected arrangements in their nuchals, and were thus classified as "other" in protocol terms, and are treated individually, below.

The six anomalous dwarf-crocodiles are not yet understood, and deserve their own special publications because both the transverse (see next paragraph and Figure 3.2) and the lengthwise (see text below Figure 3.2 and Figure 3.3) fusions are probably totally unknown in both the living and fossil crocodilians, and thus are real news of special interest to anatomists and vertebrate palaeontologists, and to C.I.T.E.S. also (these animals do not key to their name, because their nuchals were found to be wrong = not known about until this thesis).

While Ross + Mayer (1983:319) said that the two anterior and obligate transverse rows of nuchals should always have two scales in it, some of the Zoer expedition specimens have the left and right scales in the pair fully fused and compounded across the midline to form a single scale that has the same dimensions as the ancestral pair had together (see Figure 3.2). In these cases, the neck muscles have the same amount of bony protection as when (theoretically) the row was composed of two scales.

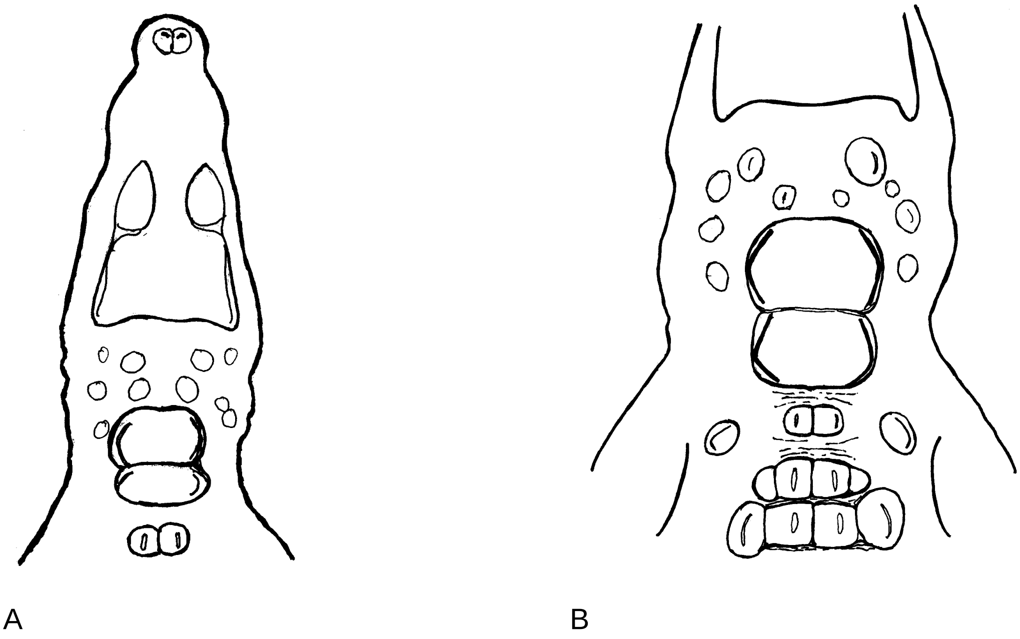


Figure 3.2 Transverse fusions of nuchals

The transverse fusions in the anterior two rows of the cervical shield occur in two African dwarf-crocodiles from the Zoer 2006-2007 sample: A = an animal (XXL-116, sex unknown) from the Likouala River (Congo-Brazzaville), and B = a male (XXL-119) also from the Likouala River (Congo-Brazzaville).

One interpretation of the observed transverse fusions in the anterior two rows of the cervical shield of *Osteolaemus tetraspis* Cope is that the covering of the muscles is important to the animal, but the exact configuration of the bone that accomplishes the job is not important to the African dwarf-crocodile species. This applies to the Figure 3.2 animals, and applies perhaps even more to the Figure 3.3 unexpected oddities.

While Ross + Mayer (1983:319) said that the two larger rows of the possible three transverse rows of nuchals in the cervical shield are always present, some individuals among the 68 dwarf-crocodiles in the Zoer 2006-2007 *Osteolaemus* sample have the anterior and posterior obligate transverse rows (the normally two, big pairs of nuchal scales) fused together in various ways (one example is illustrated in Figure 3.3, below).

Figure 3.3 Lengthwise fusion of nuchals

In this animal with no-sex (XXL-157) from Cameroon at Yaoundé, the anterior and posterior obligate transverse rows are lengthwise fused together on both the left and right hand sides.

The Zoer 2006-2007 Africa expedition encountered several manifestations of abnormal nuchal scales. Apart from transverse and lengthwise fusion of nuchals, the nuchal scales can also be anomalous, meaning lacking bilateral symmetry. Two African dwarf-crocodiles with anomalous nuchal scales on their neck are presented in Figure 3.4, below.

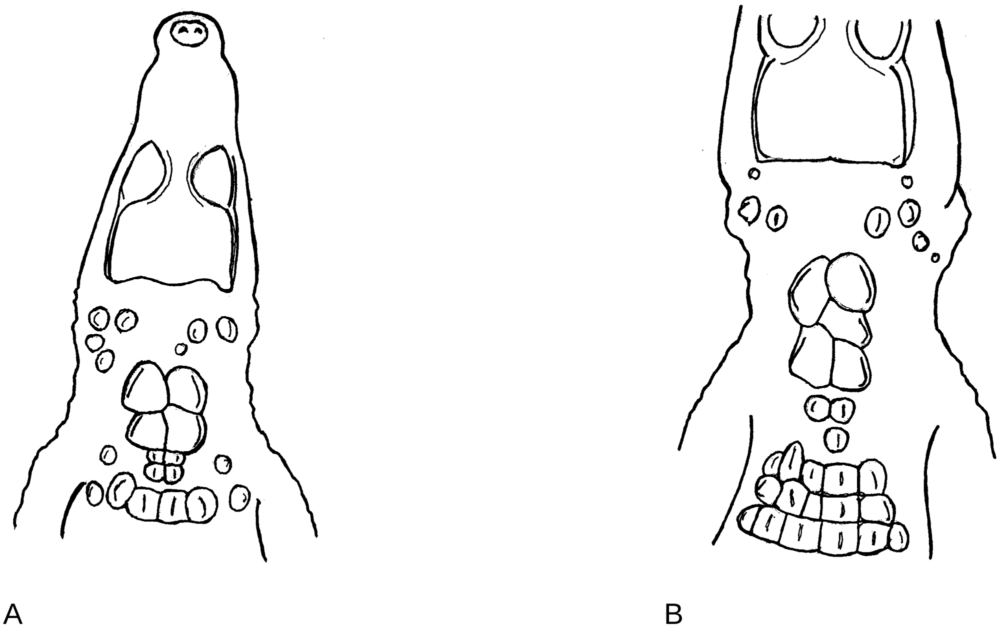


Figure 3.4 Two examples of anomalous nuchals

Two examples of African dwarf-crocodiles with anomalous nuchal scales: A = *Osteolaemus* from the Likouala River (Ubangi River drainage, Congo-Brazzaville INTERIOR), and B = *Osteolaemus* from Congo-Brazzaville at Pointe-Noire COAST.

In cases of anomalous nuchals, or fusions of nuchals (transverse and lengthwise), it is not possible to compare the lengths of the separate nuchal rows of the cervical shield. However, the length of nuchals without fusion and anomalous scales can be compared to see if this scale-count supports the C.I.T.E.S. recognition of *Osteolaemus tetraspis osborni* (K.P. Schmidt). The normal condition of the nuchals is discussed below in Subsections 3.3.1 (lengths of obligate rows) and 3.3.2 (presence or absence of the optional third and posteriormost transverse row of nuchal scales in the cervical shield on the neck of the African dwarf-crocodile).

3.3.1 The anterior pair of nuchal scales is either longer than, or equal in length with, or shorter than the middle transverse row of a possible three transverse pairs of nuchal scales

While Ross + Mayer (1983:319) said that the first (from the head) transverse row in the *Osteolaemus tetraspis* cervical shield is usually longer (in the head to tail direction) than the middle row (the obligate second pair of nuchals), the 1983 statement allowed for at least slight variation in this character, where, for example, both of the obligate rows are essentially equal in length, or the posterior of the two is only very slightly longer than its anterior neighbour.

However, the prediction in Ross + Mayer (1983:319) was for the overwhelming majority of African dwarf-crocodiles to have the anterior obligate row slightly longer than the obligate row immediately posterior to it, the middle row of the possible three transverse rows of nuchal scales in the cervical shield. The 1983 Harvard University study essentially said that the anterior row is the longest, the middle row is slightly shorter, and the third and posteriormost possible transverse row in the cervical shield is always considerably the shortest of the three. The Ross + Mayer (1983:319) assertion that the third row is vestigial and sometimes completely absent appears to be true (see Subsection 3.3.2), but Figure 3.5 and Table 3.2 will test and expand the limits of known variation in the relative lengths of the two anterior rows of nuchals (transverse pairs of scales) in the Zoer 2006-2007 sample.

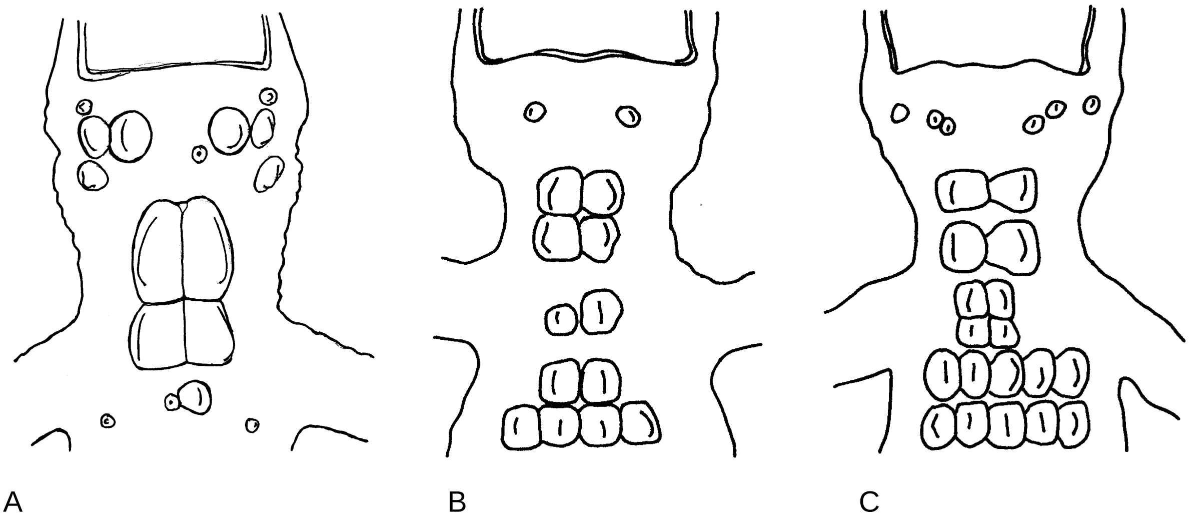


Figure 3.5 First pair of nuchals can be longer than, or equally long as, or shorter than the second pair (anterior to posterior)

Three male African dwarf-crocodiles with different ratios between the two obligate rows of the cervical shield: A = XXL-137 from Gabon at Setté Cama COAST; B = XXL-183 from Cameroon at Mundemba COAST; and C = XXL-109 from Congo-Brazzaville at Bellelo COAST.

The Zoer 2006-2007 field-collected *Osteolaemus* sample (n=68 with locality data, and in many cases sex data also) is the largest ever assembled for African dwarf-crocodiles. Published photographs and drawings of the cervical shield in the African dwarf-crocodile usually show the Figure 3.5-A condition where the anteriormost transverse-row of nuchal scales is slightly longer, along the long-axis of the animal, than its posterior obligate neighbouring row. There are 61 animals with nuchals that are suitable for C.I.T.E.S. analysis, which will now be reported in Table 3.2 and several other tables (below).

Table 3.2 Comparison in length of the two obligate anterior nuchal rows

Questions about the length of the nuchals	frequency
Anterior row longer than middle row	55 out of 61
Anterior row length equal to middle row	2 out of 61
Anterior row shorter than middle row	4 out of 61

As mentioned in Table 3.1 (above) only 61 African dwarf-crocodile neck-shields were suitable for analysis using the Ross + Mayer (1983) model. In the vast majority (55 out of 61 animals) the anteriormost nuchal row is longer than the second obligate row posterior to it.

However, in four animals from this 2006-2007 sample, the anterior row is shorter than the middle row. In two animals, the two obligate anterior rows are equal in length.

These results about the length of the two obligate anterior nuchal rows are to be tested for geographic variation and for variation correlated with sex. In Table 3.3 the geographic variation hypothesis is tested amongst localities, and the sex-variable hypothesis will be tested in Table 3.4, below.

Table 3.3 Cases where most anterior nuchals-row is the longest

Locality detail and geographic-kind	frequency in locality (n=61)
Porto Novo = COAST subspecies	1 out of 1 in Benin
Yaoundé = COAST subspecies	14 out of 29 in Cameroon
Mundemba = COAST subspecies	2 out of 29 in Cameroon
Campo Maan = COAST subspecies	8 out of 29 in Cameroon
Five animals from Cameroon were found to be different	
Setté Cama = COAST subspecies	5 out of 6 in Gabon
Kango = COAST subspecies	1 out of 6 in Gabon
Locality detail and geographic-kind	frequency in locality (n=61)
Pointe-Noire = COAST subspecies	5 out of 11 in coastal-Congo
Youbi = COAST subspecies	1 out of 11 in coastal-Congo
Dembouanou = COAST subspecies	1 out of 11 in coastal-Congo
Bellelo = COAST subspecies	3 out of 11 in coastal-Congo
Almost all of the Congo-Brazzaville coastal sample were longer, but one of the eleven (a Bellelo animal) was shorter	
Likouala = INTERIOR subspecies	13 out of 13 in interior-Congo
Kinshasa = INTERIOR subspecies	1 out of 1 in Zaïre-DRC

Table 3.3 contains African dwarf-crocodiles on which the anterior nuchals-row is longer than the middle pair of scales of the cervical shield. The six localities of the 2006-2007 sample are present in this table. All COAST localities are *Osteolaemus tetraspis tetraspis* Cope, while the two INTERIOR locations are the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies. It is notoriously difficult to make generalizations about the neck scales on any

crocodilian, and the African dwarf-crocodile confirms the predicted unpredictability about nuchals.

In six of the coastal animals, the most anterior nuchals-row is not longer than the middle pair of nuchals. The most anterior nuchal-row is the longest in the majority of the animals, both COAST and INTERIOR. The sex-variable hypothesis will be tested in Table 3.4 as another possibility for correlating the lengths of the obligate nuchals character with biology, other than the hypothesis that in *Osteolaemus tetraspis* Cope the interscale-fusion details do not matter to the animal as long as the obligate nuchals are present (Section 3.3 above). Anomalous cervical shields occurred in adults that looked as though they were healthy and successful before being captured by humans. One specimen appeared to have its cervical scales damaged by humans (XXL-130 female from Gabon at Kango COAST). By coincidence, all six of the “anomalous” African dwarf-crocodiles excluded from the nuchals sample were without sex-data (XXL-139 from Gabon at Gamba COAST; and XXL-153, #156, and XXL-157 Cameroon at Yaoundé COAST; and XXL-181 Cameroon at Limbe COAST; and lastly XXL-115 Congo-Brazzaville at Likouala INTERIOR).

Table 3.4 Lengths of obligate nuchals sex-data examined

Locality and subspecies	anterior row	frequency and country	sex
Porto Novo = COAST (#185)	longer	1 out of 1 from Benin	no
---	---	---	---
Kango & Setté Cama COAST	longer	6 out of 6 from Gabon	A
---	---	---	---
Mundemba, Yaoundé, and Campo Maan = COAST	longer	24 out of 29 Cameroon	B
Mundemba & Limbe COAST	equal-to	2 out of 29 Cameroon	C
Yaoundé = COAST	shorter	3 out of 29 Cameroon	D
---	---	---	---
Locality and subspecies	anterior row	frequency and country	sex
Bellelo, Pointe-Noire, Youbi, and Dembouanou = COAST	longer	10 out of 11 Congo-B	E
Bellelo = COAST (#109)	shorter	1 out of 11 Congo-B	male
Likouala = INTERIOR	longer	13 out of 13 Congo-B	F
Kinshasa = INTERIOR (#17)	longer	1 out of 1 Zaïre-DRC	female

In Table 3.4 the lengths of the obligate nuchals of African dwarf-crocodiles are sex-data examined. As mentioned above, the anterior obligate row can be longer, equal to, or shorter than the middle (and obligate) pair of nuchals. The letters in the sex column are explained below.

The letters in the sex column of Table 3.4 (above) mean: A = XXL-132 male, #s 134-135 females, #s 136-137 males, #138 female; and B = #s 148, 150-152, 154-155, and 158 all with no-sex, 160 male, 161 female, 162 male, 163-164 no-sex, 165 male, 166-167 females, 170 male, 171-172 females, 173 male, 174-175 females, 176 no-sex, 182 female, 184 male; and C = #s 180 no-sex, 183 male; and D = #s 149 no-sex, 159 no-sex, 169 male; and E = #s 104-105 no-sex, #s 106-107 females, #108 male, #s 124-125 males, #s 126-127 no-sex, #128 male; and F = #s 110-111 males, 112 female, 113-114 no-sex, 116-117 no-sex, 118-121 males, 122-123 females. The three single animals in Table 3.4 cancel each other out, being one male, one female and one with no data. The letters mean: A = 6 with sex from Gabon (3 males, 3 females); B = 14 with sex from Cameroon (6 males, 8 females); C = 1 more Cameroon with sex (male); D = 1 more Cameroon with sex (male); E = 6 with sex from Congo-Brazzaville coast (4 males, 2 female); and F = 9 with sex Congo-Brazzaville interior (6 males, 3 females).

The sex ratio (when known = random) appears random about which sex has the anterior obligate transverse row of nuchals longer (along the long-axis of the animal) than its posterior obligate neighbour. The third and posteriormost possible transverse row of nuchal scales in the cervical shield is discussed in Subsection 3.3.2 below.

3.3.2 Posterior optional shortest row with zero, or one or two scales

According to Ross + Mayer (1983:319), there should be a small transverse space of flexible and unarmoured skin immediately posterior to the second obligate pair of nuchal scales in the cervical shield of *Osteolaemus tetraspis* Cope. Immediately posterior to this small space of bare skin inside the cervical shield, some remnants or even all of the optional third pair of nuchal scales can occur, or alternatively they can be absent, or only present in widely separated parts (a vestigial condition that does not count). There are thus two questions about this most posterior of the possible cervical rows: is it present or absent? And, if present, how many scales are in the transverse row?

The third and most posterior possible transverse row of cervical scales on the African dwarf-crocodiles is the most variable of the three pairs of nuchals (Ross + Mayer 1983:319), and this optional row can at times be remarkably difficult to identify and study for two reasons. It is polymorphic (two, one, or zero scales are possible). Additionally, it often looks almost exactly like the thoracic transverse row immediately posterior to it, which is often reduced to two thoracic scales. For details about the anterior end of the dorsal body armour as it approaches the base of the neck, see Chapter 7 (below) about "PC-18" and the cervico-thoracic juncture.

Because the most posterior possible transverse row of neck scales often resembles the most anterior transverse row of thoracic scales, Ross + Mayer (1983:319) mentioned that the optional cervical row, if present, should have (in addition to the strip of skin anterior to it) a small transverse strip of flexible and unarmoured skin immediately posterior to it, narrowly separating the cervical shield from the thoracic dorsal armour series. The 1983 hint from Harvard (Ross + Mayer 1983), that the optional third row of the neck shield is the one that has skin both anterior and posterior to it, is apparently an oversimplification caused by small sample size, because the Zoer 2006-2007 sample of 68 African dwarf-crocodiles included some specimens where the most anterior thoracic row was also with a flexible space of skin both anterior and posterior to it. In other words, there are *Osteolaemus tetraspis* Cope which have an extra and unexpected third transverse strip of bare skin crossing the dorsal long-axis midline of the animal, and Figure 3.6 shows an example.

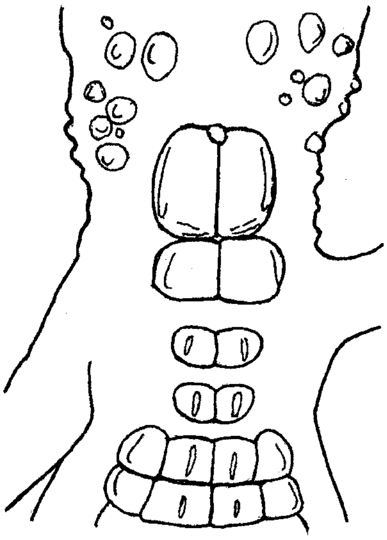


Figure 3.6 Variation in skin in between anteriormost precaudal rows

In African dwarf-crocodiles, variation in skin located physically between the anteriormost precaudal rows occurs. This male (XXL-165) in Figure 3.6 from Cameroon at Campo Maan COAST has skin in between PC-17 and PC-18, and also skin in between PC-18 and PC-19, and also skin in between PC-19 and the obligate nuchals.

The Figure 3.6 phenomenon (above) of having a third and unexpected transverse strip of flexible skin separating the two most anterior of the thoracic transverse rows of dorsal body armour is analysed and tested for geographic variation in Chapter 7. This is done because of the special Ross + Mayer (1983) technique for correlating the transverse rows of thoracic scales with their underlying vertebrae, and thus assigning identification numbers to the scale rows. This method is introduced in Chapter 5 about locating the “sacro-caudal juncture” transverse division-line between the crocodile’s body and its tail, and then the technique is applied to the sacral, lumbar and thoracic dorsal-armour of the genus *Osteolaemus* Cope, 1861, in Chapter 7.

The sometimes present third possible transverse space of flexible skin in Figure 3.6 (above) can, in theory, sometimes be the actual second of two such spaces, when the optional most-posterior pair of nuchals in the cervical shield is completely missing. Again, these special cases and variations in the region where the dwarf-crocodile’s body articulates with its neck are postponed until Chapter 7 (below), because ambiguity in the cervico-thoracic juncture region is resolved by approaching the problem from the other direction. Until now, everything has been progressing from the head toward the tail, but beginning with Chapter 5 (below) and continuing in Chapter 7 (below), the crocodile’s pelvis will become the defined point from which the thoracic rows get their identifying vertebral correspondence numbers, such as “PC-18” (the 18th transverse row from the tail) and “PC-17” (the 17th precaudal row). In Section 3.2 (and Figure 3.6) an extra and unexpected transverse narrow space of unarmoured skin occurs between precaudal row 17 and precaudal row 18 (see also Chapters 5 and 7).

One explanation for an extra space of flexible skin unexpectedly developing within the anterior thoracic zone of the dorsal armour in *Osteolaemus tetraspis* Cope is as compensation for flexibility lost in the African dwarf-crocodile’s cervical shield (the fusion phenomenon in and among the obligate two pairs). Even when no fusion of obligate nuchal-scales occurs, the roughly and remarkably square dorsal-view shape of the four individual obligate scales in the cervical shield in this species creates the total effect of an unusually stiff and bony rectangle extending along the long-axis of the neck for a considerable distance. This loss of flexibility in the neck should, in theory, require compensation in the thoracic zone, because the animal needs to have a certain amount of total body flexibility.

An additional way for the African dwarf-crocodile to achieve flexibility in the cervico-thoracic junction region is the reduction and deletion of the optional transverse row of nuchal scales in the cervical shield. Variation in this condition is documented in Table 3.5 (below). It is essential for a crocodilian to bend its body for defending its pelvic and abdominal regions from predators, and also for cleaning its eyes and ears and its teeth with the toenails on the back feet. Further, the embryo is bent inside the egg.

Table 3.5 Variation in the presence or absence of the optional transverse row of posteriormost cervical scales

Three character states	occurrence rate
Optional pair of two nuchal scales present	45 out of 68
Optional nuchals reduced in number to one scale	0 out of 68
The optional row of nuchals is functionally absent	23 out of 68

In the vast majority of the African dwarf-crocodiles from the Zoer 2006-2007 sample the optional pair of nuchals is present. Twenty-three animals have the optional row of posteriormost cervical scales absent.

The prediction of Ross + Mayer (1983:319) was that *Osteolaemus tetraspis* should have a fold of skin anterior to PC-18 followed by (anterior to it) a row of two small elements (PC-19), and then another fold of skin followed in the anterior direction by two rows of two large elements each (obligate nuchals). Ross + Mayer’s (1983:fig. 9A) shows that PC-19 can also be missing. Note that all African dwarf-crocodiles in this Zoer 2006-2007 sample lack any one-scaled PC-19’s.

The sex of the forty-five (45) African dwarf-crocodiles with the optional nuchals present is at the following localities: Benin represented by one female specimen; Cameroon (18 out of 45) represented by six males, four females, and eight specimens with no sex data; Gabon (4 out of 45) represented by two males and two females; Congo-Brazzaville COAST (8 out of 45) represented by four males, two females, and two specimens with no sex data; Congo-Brazzaville INTERIOR (13 out of 45) represented by six males, two females, and five with no sex data; and one female specimen from Zaïre-DRC INTERIOR. In total there are 18 males, 11 females, and 16 specimens with no sex data.

Note that all of the characters in Chapter 2 and Chapter 3 are dorsal armour that ossifies into bony keeled scutes in the adult of *Osteolaemus tetraspis* Cope, as compared with the next chapter (Chapter 4: the collar-vent count and the transverse scale-count across the widest part of the belly) which physically turns the African dwarf-crocodile over (onto its back, with its belly up) and examines the ventral scales, very few of which ossify in the adult, and all of which are flat (lacking a keel).

3.4 REVIEWING THE NUCHAL SCALES

The relatively rare and totally unexpected cases where fusions (co-ossifications) occur among the individual pairs of nuchals scales on the dorsal surface of the neck in *Osteolaemus tetraspis* Cope (as a species) are mostly concentrated in one INTERIOR locality (Likouala River). However, anomalous nuchals, and also partial fusions between nuchals scales, can also be found in COAST animals. Thus, because they are uncommon in nature, and because fused nuchals are an extremely variable phenomenon by definition, it seems unwise to characterize any African dwarf-crocodile subspecies by the presence or absence of these various kinds of fusions (and sometimes associated bilateral asymmetry) that are newly discovered to occur in the nuchals scales on the neck. The majority of the Zoer 2006-2007 African dwarf-crocodile sample agrees with the prediction about *Osteolaemus* nuchals in Ross + Mayer (1983), with the notable exception that the optional row (PC-19) occurs considerably less frequently than was observed in the Ross + Mayer (1983) smaller total sample of *Osteolaemus tetraspis*. Another deviation from the Ross + Mayer (1983:319) characterization of the obligate four nuchals scales in *Osteolaemus* Cope is that the anteriormost row of nuchals is sometimes considerably shorter than the posterior row of the obligates. This latter phenomenon occurs only in *Osteolaemus tetraspis tetraspis* when the COAST and INTERIOR subspecies are defined the way that C.I.T.E.S. has traditionally mapped the geographic ranges of these two taxa.

CHAPTER IV TWO KINDS OF VENTRAL SCALATION CHARACTERS FOR BELLY SKINS

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

4.1 INTRODUCTION

While the two preceding (and also five later) chapters are all scalation characters from the dorsal armour of African dwarf-crocodiles, the subject here in Chapter 4 involves two ventral characters on the belly of *Osteolaemus*. The question: “What African dwarf-crocodile scale-counts best support C.I.T.E.S. recognition of *Osteolaemus tetraspis osborni* (K.P. Schmidt)?” can possibly be answered with data about these two scale-count characters from the belly. Does the collar-vent count, and-or the number of transverse scales across the widest part of the belly in *Osteolaemus* support the C.I.T.E.S. hypothesis? In this chapter the collar-vent count, and also the number of scales in selected transverse belly-rows are discussed.

In this chapter the results of the characters on the belly will be presented for each nation sampled. Countries where the 2006-2007 expedition conducted research on the belly of the African dwarf-crocodile was restricted to Cameroon, Gabon, Congo-Brazzaville and Zaïre-DRC. The results of the African dwarf-crocodile belly scale-counts are presented nation by nation in tables. This format is used in every chapter of this thesis in which any kind of potential identification character is discussed.

Similarly, a comparison here is made between specimens from the equatorial Atlantic coast nations, as compared with animals from far inland in central Africa. In this case, Cameroon, Gabon and Congo-Brazzaville (equatorial Atlantic coast) all got the label (place indication) “COAST” (meaning *O. t. tetraspis*), while in contrast, Congo-Brazzaville (Ubangi River region) and Zaïre-DRC got the label “INTERIOR” (meaning *O. t. osborni*).

Before the Zoer 2006-2007 sample of *Osteolaemus tetraspis* data was collected in the relevant zone of equatorial Africa, there were five published sources of collar-vent (C-V) numbers for each of the two C.I.T.E.S. subspecies. The most recent of the five papers (Fuchs, 2006:133, 136) claimed that the COAST taxon can always be distinguished from the INTERIOR taxon, because there is no overlap in their C-V scale-counts. In this case, *Osteolaemus t. tetraspis* from the C.I.T.E.S. coastal region have 25 to 29 transverse rows of ventral scales between the throat collar and the cloacal-vent oval. In contrast, Fuchs (2006) reported 22 to 24 rows in the collar-vent count for the INTERIOR (*O. t. osborni*) subspecies of African dwarf-crocodile. Thus, none of the COAST animals should have 24 of the C-V rows; and none of the INTERIOR subspecies taxon should have 25 of the C-V rows.

It appears from the data in Fuchs (2006:132-137) that a commercial belly-skin of *Osteolaemus tetraspis* that is lacking its head, and is also lacking its dorsal armour, can still be reliably identified to subspecies by collar-vent numbers. However, the exact method that Karlheinz Fuchs (2006) employed for calculating his data was not adequately explained, and it is likely that his C-V count was made once, and directly along the midline, which King + Brazaitis (1971:18) found to have problems. Rather, the New York Zoological Society team of Wayne King and Peter Brazaitis employed a recommended method of counting the number of collar-vent (C-V) rows in a parallel fashion (below).

Further, the exact and precise anterior and posterior ends of the collar-vent (C-V) scale-count character in Fuchs (2006) are not defined clearly enough to be repeated by other scientists.

Lastly, the Fuchs (2006) sample-size, for both of his African dwarf-crocodile subspecies, is unknown. The material studied by tannery engineer K. Fuchs (2006) was entirely commercial belly hides, and thus their precise geographical locality data is suspect, and probably vague, being nation-of-origin only.

Before Fuchs (2006), the Charette (1995) identification guide for C.I.T.E.S. claimed the same separation between the C-V counts for the COAST and the INTERIOR taxa. However, rather than Fuchs (2006) repeating data from Charette (1995), the prediction that COAST = 25 to 29 transverse rows in the collar-vent scale count, compared with INTERIOR predicted to be 22 to 24 collar-vent rows, had earlier appeared in the first edition of his book (Fuchs, 1974, in German). Thus Fuchs (2006:133, 136) probably followed Fuchs (1974:168, 172); and, Charette (1995:orange 9) did so also.

The Charette (1995:green 4) does not employ the King + Brazaitis (1971:18) method of counting the number of C-V rows twice (= two times), parallel to, but one ventral-scale away from the long-axis crocodilian midline, in a conscious effort to avoid ventral midline anomalies of one scale each, and also to avoid confusing zipper-like zig-zags that do not affect the real count of transverse rows that properly cross the midline.

Before Charette (1995), there was an existing and alternative set of collar-vent (C-V) numbers for *Osteolaemus tetraspis* subspecies in Brazaitis (1973:79), which were calculated the King + Brazaitis (1971) way, which is slightly different from the Fuchs (1974, 2006) and C.I.T.E.S. method in Charette (1995). In detail, according to Brazaitis (1973:79) the COAST taxon has 26 to 27 rows of C-V scales, while the INTERIOR subspecies has 21 to 23 transverse rows of ventral scales in its collar-vent count. The sample size for *Osteolaemus* in Brazaitis (1973:79-80) was not given, but can be assumed to be small (n=3 or less) for the *Osteolaemus tetraspis osborni* (Schmidt) taxon. However, the geographic data for some of the INTERIOR sample in Brazaitis (1973) was from the type locality, and the only theoretical problem with this method of parallel counting is that all of the C-V data in Brazaitis (1973) is reported in whole numbers. Thus, it is unclear about how 24 on the left-side, and 25 on the right-side, would be reported. Logic demands 24,5 as the result.

Despite its minor mathematical problem, the Brazaitis (1973) method, which is really the King + Brazaitis (1971:18) method, is probably more repeatable. Further, many of the specimens that W. King and P. Brazaitis examined are still in museum collections, and thus can be examined for clarity. In contrast, all of the material that was reported in Fuchs (1974) and Fuchs (2006), and presumably Charette (1995) also, has been made into leather products, and sold.

It is interesting that while Brazaitis (1973:79) found separation in C-V counts between the two taxa, the earlier King + Brazaitis (1971) data did not make that assertion. Rather, according to King + Brazaitis (1971:26), the COAST had 21 to 27 rows, and the INTERIOR also had 21 to 27 transverse rows of ventral scales in the C-V count. Note that 21 does not occur on *Osteolaemus tetraspis* as a species, according to Fuchs (1974, 2006) or Charette (1995), but Wayne King and Peter Brazaitis in New York City and the Bronx Zoo definitely recorded 21 rows in the collar-vent character.

The gular collar is located on the ventral surface between the front legs, and usually includes several conspicuously enlarged scales near the animal’s long-axis midline. This throat-collar often includes some irregularly shaped scales, and is sometimes difficult to find on some crocodilian taxa, but the collar was always reasonably distinct in the 2006-2007 sample of *Osteolaemus*, and is also characterized as “a single transverse row of enlarged scales” in the literature. Note that the collar is not itself included in the collar-vent count of transverse rows on the belly. Rather, the gular (throat) collar is the landmark that identifies the first transverse row that is posterior to the collar, as indicated on Figure 4.1 (below) with arrows.

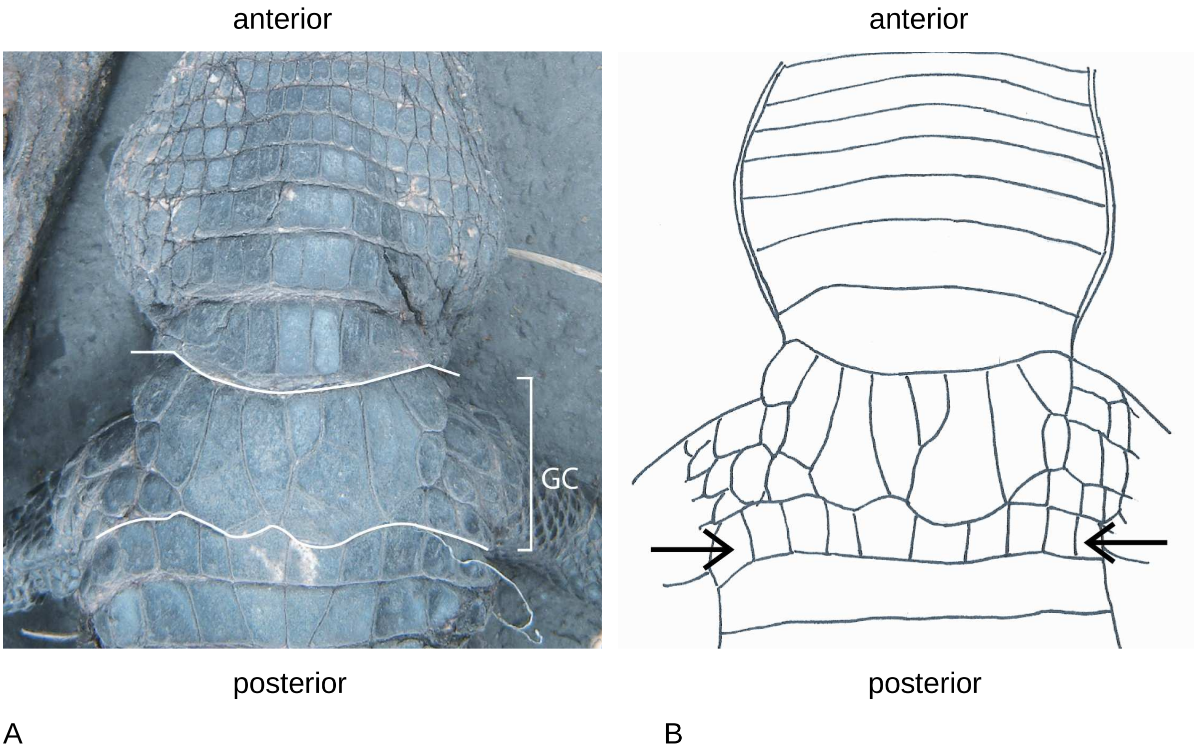


Figure 4.1 The gular collar

The photo on the left hand side (4.1 A), and the drawing on the right-side (4.1 B), show the gular collar (= GC) on a male *Osteolaemus* (XXL-111) from Congo-Brazzaville at Likouala (= INTERIOR). Note that the Likouala River animals were physically examined in the bushmeat market in Brazzaville, and their locality data was obtained verbally from reliable informants. The arrows on the drawing indicate the first transverse row of ventral scales that is posterior to the collar.

The first transverse row of scales posterior to the collar is the anterior end of the collar-vent (C-V) count, and this anteriormost belly-row is included in the C-V result. Similarly defined, but in the opposite direction, the first transverse row of belly scales that crosses the midline at a level anterior to the cloacal-vent “oval” (the other end of it is sometimes U-shaped) is included in the C-V count. Thus, the C-V count is between the collar and the vent, but not including them. Note that in *Osteolaemus* and many other crocodilians, the task of deciding where the cloacal disturbance has its anterior edge is not easy. Some authors define the cloacal obstruction as an encircling row of small scales adjacent to the cloacal slit, but this is an oversimplification. The 2006-2007 field-protocol applied both definitions, and based on granular scales bordering the opening of the cloaca (the slit), and also based on the contiguous scales in a transverse row, the posteriormost row that is counted in the C-V count is indicated on Figure 4.2 B (below) with arrows.

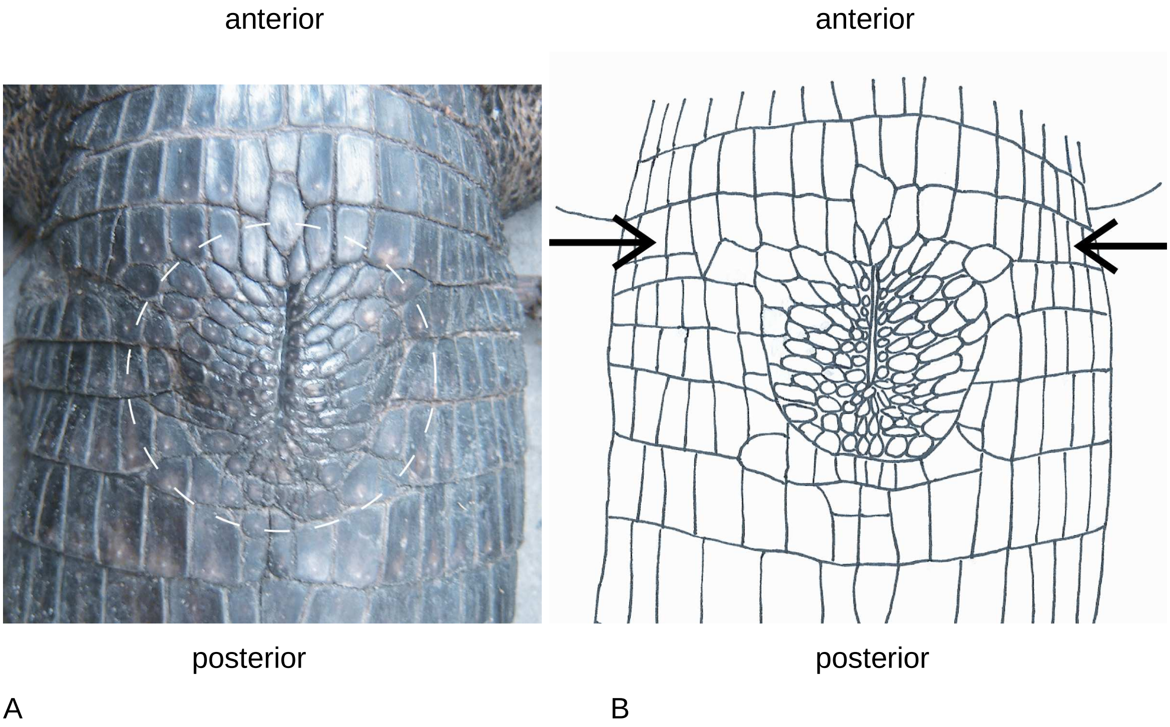


Figure 4.2 The cloacal-vent oval

Both the photo (4.2 A), and the drawing (4.2 B), show the cloacal-vent oval of a male African dwarf-crocodile (XXL-118) from Congo-Brazzaville at Likouala (= INTERIOR), examined at the bushmeat market in Brazzaville. The posteriormost belly-row to pass unbroken across the anterior end of the cloacal vent is included in the collar-vent count. This transverse row of ventral scales is indicated in the drawing by arrows.

The second character in this chapter is the maximum number of ventral scales in a transverse row crossing the widest level of the belly, located approximately half way between the throat collar and the cloacal vent oval. This is an independent variable, and is not believed to be directly correlated with the collar-vent (C-V) character in any way in the Crocodylia as a whole, as exemplified by the living species.

Unfortunately the lateral (distal) ends of the scale count across the belly are poorly defined in the literature. The transition between ventral scales and lateral (flank) scales is often slightly different in details, and this causes problems when comparing many different and diverse taxa with each other. Perhaps for this reason, or for whatever reason, it is notable that King + Brazaitis (1971), and also Brazaitis (1973), did not present data for this second character that at first-sight appears to be available on the commercial belly-skin that C.I.T.E.S. regulates in trade most heavily.

Because King + Brazaitis (1971), and also Brazaitis (1973), were written in anticipation of the C.I.T.E.S. need to identify commercial belly-hides, it can be assumed that these two American papers considered the possibility of performing the transverse maximum ventral scale-count, and rejected it for practical reasons. The method of identifying the lateral (distal) ends of the truly “ventral” special scales is too complicated, and the probability of repeating results is low, especially in cases where highly dissimilar crocodilian taxa are examined, such as (for example) the Indian gharial being compared with a dwarf-cayman form South America. However, this difficulty becomes far less important when only a single species (or adjacent subspecies) are reported, because when closely related taxa are compared, it is possible to more precisely define the dividing line between truly “ventral” scales and those that are flank-scales adjacent to them, and more distal.

There are three existing publications of data about the number of ventral scales in the widest (= longest transverse series) row across the belly. Similar to the C-V counts, the data for the across-the-belly character in Fuchs (2006:133, 136) is the same exact numbers as in Fuchs (1974:168, 172), and also Charette (1995:orange 9). Thus, from a sample of unknown size, the COAST (*O. t. tetraspis*) is 10 to 12 ventrals across, as compared with 12 to 14 scales in INTERIOR (*O. t. osborni*) animals.

4.2 METHODS

The two belly counts recorded by the Zoer 2006-2007 African dwarf-crocodile expedition are discussed as two separate characters, and for both scale-counts the methods are illustrated in figures below. The collar-vent count on the belly is discussed first, because the literature suggests that it has the highest probability of success at distinguishing these two subspecies.

4.2.1 The collar-vent count on the belly

The collar-vent (C-V) count is the result of an average of two parallel counts on the belly. The number of rows between the gular collar and the cloacal oval are counted on both the left and the right sides of the ventral long-axis midline. Then, the two C-V results are added together, and later the result is divided by two, to produce a median (average) number. This method with the collar-vent count being an average of the two parallel belly-counts in the African dwarf-crocodile is made approximately one scale away from the long-axis ventral midline. The individual scales in 22 of the 23 transverse C-V rows on one *Osteolaemus* belly are omitted in Figure 4.3 (below), to make the counting of the left and right sides easier.

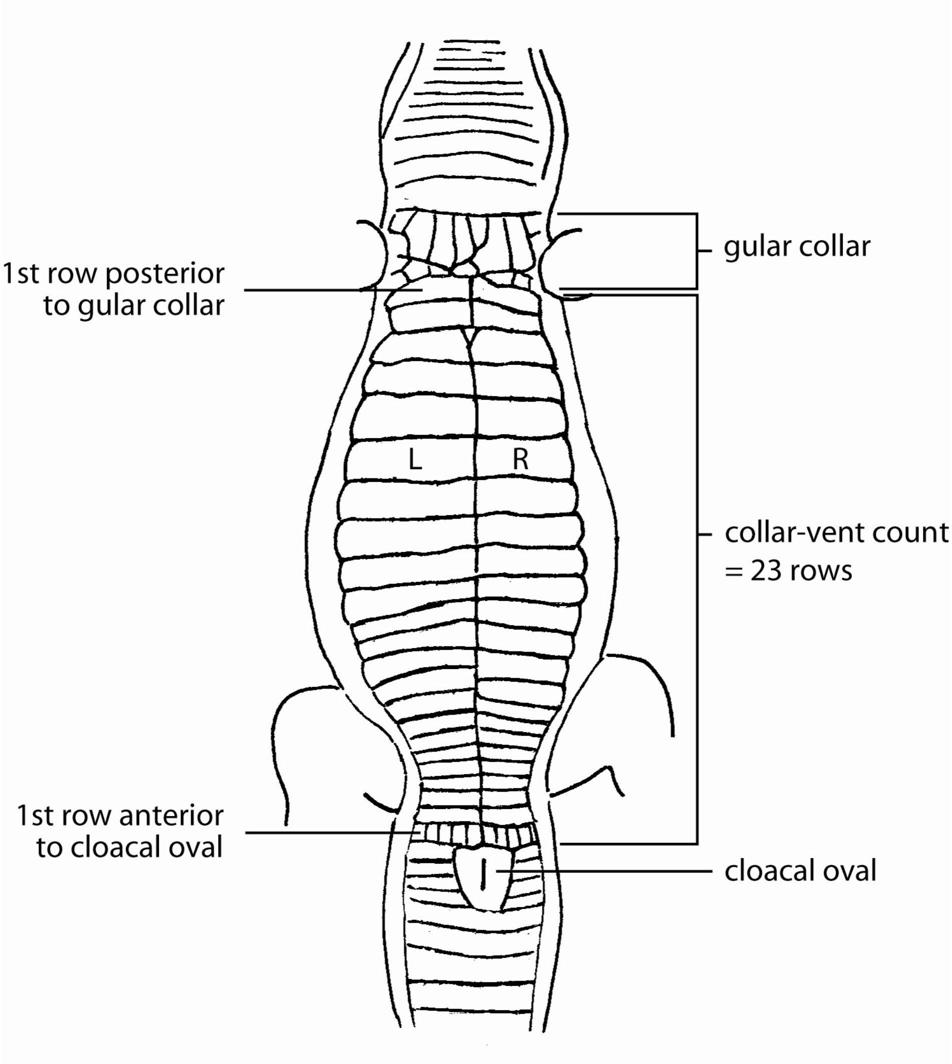


Figure 4.3   Collar-vent (C-V) count on the belly

On this male specimen (XXL-118) from Congo-Brazzaville INTERIOR at Likouala River, the collar-vent count is twenty-three (23) rows. This *Osteolaemus tetraspis osborni* (K.P. Schmidt) is 147 cm in length. The 1st belly row anterior to the cloacal oval is indicated in this figure, as is also the 1st belly row posterior to the gular collar. Both the left side and also the right side of the belly consist of 23 rows from collar to vent on this African dwarf-crocodile. This figured individual *Osteolaemus tetraspis* is bilaterally symmetrical in the number of transverse rows. Note that there is an isolated one-scale anomaly along the midline (in the thoracic region) which would produce a count of 24 rows if the parallel method was not utilized on this animal. Further note that the posterior edge of the throat collar is subject to varying (subjective) interpretations, and thus it is possible that the Charette (1995) method would produce a C-V count (their “TR” character) of 25 scales along the long-axis ventral midline.

4.2.2 Counting the ventral scales in a transverse row across the widest part of the belly

The second major kind of scale-count on the belly that was recorded by the Zoer 2006-2007 expedition is the number of ventral scales in a transverse row across the widest part of the belly. The method for counting these scales is illustrated in Figure 4.4 below. Note that this character is called “lengthwise rows” or “longitudinal rows” (LR’s) in the 1995 C.I.T.E.S. guide, but the ventral scales on the modern (eusuchian) crocodilian belly are usually not actually arranged in long-axis rows. It just looks like longitudinal rows in some minor regions. Thus, the C.I.T.E.S. character “transverse rows” (TR’s = C-V rows) is appropriately named, but the so-called LR’s (the second character discussed in this chapter) are really the number of truly “ventral” scales in the transverse row across the maximum mid-belly level, only.

In the literature, the ventral scales are often described as being rectangular. This is generally true, but the D-shaped scales at the distal ends of each transverse row of ventral scales are also counted as ventrals in cases where the D-shaped scale has the same anterior-posterior length as the rectangular ventral scale adjacent to it, as shown in three selected transverse mid-belly rows on an *Osteolaemus* in Figure 4.4 (below). Note that although the distal ends of these transverse rows across the belly are sometimes tricky to identify in some crocodilian taxa where the transition between the ventral scalation and the flanks scalation is gradual, this was not the case in African dwarf-crocodiles, where the lateral edge of the belly is generally obvious.

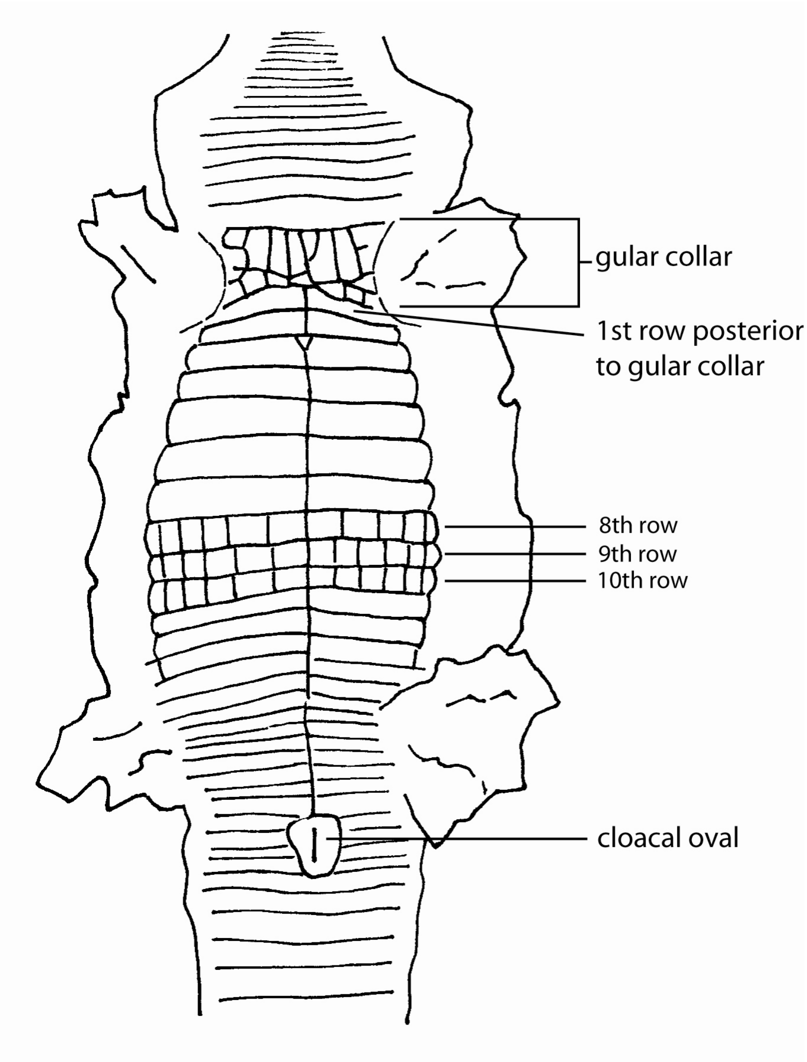


Figure 4.4 Number of transverse scales across the widest part of the belly
This male specimen from Congo-Brazzaville INTERIOR at Likouala River shows the transverse scales across the widest part of the belly. The number of transverse scales in the 8th row (11 scales), 9th row (12 scales), and 10th row (12 scales) from the gular collar are indicated. The D-shaped scales at the distal ends of the transverse rows are included in this scale-count across the belly.

These two kinds of ventral scalation characters are the only scale-counts that are available on commercial belly-hides in the international leather trade, and are thus of extreme importance to C.I.T.E.S..

4.3 RESULTS

In this section the results about the two kinds of scale-counts on the belly of African dwarf-crocodile are presented. The results from the collar-vent count are presented first, and then later, the scale-counts across the widest part of the belly, in the 8th, 9th and 10th transverse rows from the gular collar, will be discussed.

Note that the Zoer 2006-2007 expedition protocol asked for the three widest rows across the belly, and these were always the same three rows in the entire sample of n=47 African dwarf-crocodiles on which ventral scalation characters were recorded. The primary reason that the *Osteolaemus tetraspis* ventral data sample size (n=47) is significantly lower (smaller) than the n=68 for dorsal scalations (in other chapters) is that often it was not possible to obtain permission to turn a specimen onto its back. This happened at some public exhibits where dorsal data could be taken visually, and could be photographed, but the belly remained unseen. Also, the local African belief system made it often impossible to physically handle living and freshly killed dwarf-crocodiles in bushmeat markets. Foreigners (and especially wildlife biologists) were forbidden to touch meat that other people would later purchase and eat. In many places even the taking of scientific photographs was taboo. Thus, it was often necessary to pretend to not be interested in the dwarf-crocodiles at meat stalls, and to secretly make observations and gather data surreptitiously. Thus, in many instances, turning an animal over, to record its ventral scalation characters, was impossible without purchasing the entire carcass (which was against the principles of the Zoer expedition members, and was not done).

As an overview of the Zoer 2006-2007 African dwarf-crocodile ventral scalation data, animals from Cameroon, and Gabon, and the Ubangi River drainage in the interior of Congo-Brazzaville, and the Kinshasa region in the interior of Zaïre-DRC, and the coastal zone of Congo-Brazzaville, are all lumped together in Table 4.1 (below) without concern about geography or sex (to be detailed below in this chapter).

Table 4.1 Results about the collar-vent count and the number of transverse scales across the widest part of the belly (n=68)

Questions about the belly of dwarf-crocodiles	yes, in how many
Counts on the belly are recorded?	47
No results on belly counts?	21 (A)

Of a possible 68 *Osteolaemus tetraspis* Cope, only on 47 African dwarf-crocodiles was the collar-vent count, and the counts in a transverse row on the belly, recorded. The vast majority of the twenty-one animals (A), without belly data, were encountered in local markets or along the side of the road (XXL-104, #105, #126, #127, and XXL-128) from Congo-Brazzaville at Pointe-Noire COAST. Also, all but two animals from Likouala INTERIOR (XXL-110, #112, #113, #114, #115, #116, #117, #119, #120, #121, #122, and XXL-123); and, further XXL-157 from Cameroon at Yaoundé COAST; and XXL-180 and #181 from Cameroon at Limbe COAST; and lastly XXL-185 from Benin at Porto Novo) lack ventral (belly) scalation data.

Even with the twenty-one individual African dwarf-crocodiles listed in the caption of Table 4.1 (above) removed from the total *Osteolaemus tetraspis* sample, the remaining forty-seven (n=47) have complete ventral data, and they probably constitute the largest comparative taxonomic (= geographic variation, as subspecies) study of African dwarf-crocodile belly scales ever conducted (when the sample size is known). It (n=47) is far bigger than the Wayne King and Peter Brazaitis study in 1971 and 1973 in the U.S.A.; and, the work by Karlheinz Fuchs in 1974 and 2006 often lacked the precise locality-data required, and the German commercial belly-hide sample was of an unknown size.

This is a very long chapter, because more than one kind of scalation character is discussed, and also because each of these characters (the C-V count of rows, and the transverse count of ventral scales in the widest row across the belly) has been employed in prior literature that often did not include the detailed definitions that are actually required for repeatability of the scientific experiment. The Ross + Mayer (1983) paper did not address these two ventral scalation characters at all. The variation C-V and widest row numbers recorded by the 2006-2007 expedition are testing the ability of C.I.T.E.S. to 100% of the time identify any individual commercial belly-hide (ventral skin without its dorsal armour and without its head) to subspecies in *Osteolaemus tetraspis* Cope, 1861. The collar-vent (C-V) row-count that is performed parallel to the long-axis midline is the ventral scalation character that is expected to possibly provide 100% reliable subspecies identification for all randomly selected African dwarf-crocodiles. Now, the substantial sample-size (n=47) and the appropriate geographic distribution of the Zoer 2006-2007 expedition's result are detailed, starting with the C-V count in Subsection 4.3.1 (below).

4.3.1 Number of transverse scale-rows along the length of the belly, the collar-vent count

In this subsection, the collar-vent (C-V) data from forty-seven (47 total) African dwarf-crocodiles from the five localities of Cameroon (n=30), Gabon (n=8), Congo-Brazzaville COAST (n=6), Congo-Brazzaville INTERIOR (n=2) and Zaïre-DRC (n=1) is discussed. As mentioned in the section "methods" (above), the result of the collar-vent count is an average of two counts (left and right sides of the belly, one scale away from the midline). These results on the C-V count are to be tested for both geographic variation and sex variation. The geographic variation is tested amongst five localities (Congo-Brazzaville has two ecological zones), and similarly the sex-variation hypothesis is tested in several additional tables, below. The results from Cameroon are presented in Table 4.2 (below). Note that Benin nation is not represented in this section, because the single specimen from Benin at Porto Novo lacks belly count data (it was on public display as a captive, and viewed only from above).

Table 4.2 The collar-vent (C-V) count of *Osteolaemus* in Cameroon (n=30)

Locality at COAST	C-V left	C-V right	C-V average	frequency
Yaoundé & Campo Maan	22	22	22	3 out of 30
Yaoundé	22	23	22,5	2 out of 30
Campo Maan	23	22	22,5	1 out of 30
--- --- --- --- --- ---	--- --- ---	--- --- ---	--- --- --- ---	--- ---
Yaoundé	23	23	23	1 out of 30
Mundemba	24	22	23	1 out of 30
Campo Maan	22	24	23	1 out of 30
Yaoundé & Mundemba	24	23	23,5	2 out of 30
Yaoundé	23	24	23,5	1 out of 30
--- --- --- --- --- ---	--- --- ---	--- --- ---	--- --- --- ---	--- ---
Yaoundé	24	24	24	1 out of 30
Yaoundé	25	23	24	1 out of 30
Yaoundé	23	25	24	1 out of 30
Yaoundé	24	25	24,5	2 out of 30
Yaoundé & Campo Maan	25	24	24,5	2 out of 30
--- --- --- --- --- ---	--- --- ---	--- --- ---	--- --- --- ---	--- ---

Yaoundé	25	25	25	3 out of 30
Yaoundé	26	25	25,5	2 out of 30
---	---	---	---	---
Campo Maan	26	no data	26	1 out of 30
Campo Maan	25	28	26,5	1 out of 30
Campo Maan	26	27	26,5	1 out of 30
Mundemba	27	26	26,5	1 out of 30
---	---	---	---	---
Yaoundé	26	28	27	1 out of 30
Yaoundé	27	28	27,5	1 out of 30

The number of transverse scale rows on *Osteolaemus tetraspis* from Cameroon (n=30) varies between 22 and 27,5 scale rows. All possible outcomes in between these extremes are almost equally represented.

Because all thirty (30) specimens of *Osteolaemus* from Cameroon are (according to C.I.T.E.S.) from the COAST geographic zone, the predicted result in Cameroon was 25 to 29 collar-vent rows (Charette, 1995:orange 9). Clearly the Zoer 2006-2007 sample of African dwarf-crocodiles from Cameroon contradicts the C.I.T.E.S. prediction by exceeding the prescribed limit of variation expected to occur in COAST animals. In fact, approximately half of the Cameroon 2006-2007 field sample exhibits C-V numbers in the 22 to 24 range, which C.I.T.E.S. (Charette, 1995) had claimed to be diagnostic for the INTERIOR subspecies (*O. t. osborni*).

The range of variation in the collar-vent count of other coastal localities is tested in several tables below, starting with the collar-vent count of animals from Gabon. The eight examined Gabon nation animals are presented in Table 4.3 below.

Table 4.3 The collar-vent (C-V) count of *Osteolaemus* in Gabon (n=8)

Locality at COAST	C-V left	C-V right	C-V average	frequency
Setté Cama	23	24	23,5	1 out of 8
Kango	25	23	24	1 out of 8
Setté Cama	24	25	24,5	1 out of 8
Setté Cama	25	25	25	1 out of 8
Kango	26	24	25	1 out of 8
Gamba	25	no data	25	1 out of 8
Setté Cama	26	25	25,5	1 out of 8
Setté Cama	28	28	28	1 out of 8

In this table the collar-vent count results on the belly of all eight African dwarf-crocodiles from Gabon in the 2006-2007 sample are presented. The results on the C-V count in Gabon specimens (n=8) vary between 23,5 and 28 rows.

Similar to the entire nation of Cameroon being defined by C.I.T.E.S. as being COAST (*O. t. tetraspis*), so too is the nation of Gabon (Charette, 1995). Thus, the prediction was that all eight (8) *Osteolaemus* from Gabon should have 25 to 29 transverse rows of ventral scales in the collar-vent character. However, when parallel C-V counts are employed in this thesis, the result is surprising, because three out of n=8 can exhibit the C.I.T.E.S. predicted INTERIOR subspecies C-V scale-count result (because “23,5” and “24,5” both imply that 24 occurs on one side, in these cases of minimal bilateral asymmetry). Note that all instances of bilateral asymmetry in the collar-vent count in the 2006-2007 field-sample were differences of only one transverse row, but more complex and extreme variations in the left side of the belly, compared with the right side of the belly, are possible in the living Crocodylia.

The data about animals from the Ubangi River drainage in the interior of Congo-Brazzaville, the Kinshasa region in the interior of Zaïre-DRC, and the coastal zone of Congo-Brazzaville are lumped together in Table 4.4 (below), because the samples are small, and the geographic territory is contiguous, though it crosses the C.I.T.E.S. subspecies boundary.

Table 4.4 The collar-vent count of *Osteolaemus* in Congo-Brazzaville and Zaïre-DRC

Locality and subspecies	C-V left	C-V right	C-V average	frequency
Bellelo = COAST	22	22	22	1 out of 6
Bellelo = COAST	25	25	25	1 out of 6
Bellelo = COAST	24	26	25	1 out of 6
Youbi & Dembouanou = COAST	26	26	26	2 out of 6
Bellelo = COAST	26	27	26,5	1 out of 6
--- --- --- --- --- ---	--- --- ---	--- --- ---	--- --- ---	--- --- ---
Likouala = INTERIOR	22	21	21,5	1 out of 2
Likouala = INTERIOR	23	23	23	1 out of 2
--- --- --- --- --- ---	--- --- ---	--- --- ---	--- --- ---	--- --- ---
Kinshasa = INTERIOR	22	22	22	1 out of 1

The C-V count was recorded on only eight (8) African dwarf-crocodiles from Congo-Brazzaville (both COAST and INTERIOR combined) and on only one individual from Zaïre-DRC (INTERIOR). The number of transverse (C-V) scale-rows on the belly in specimens from coastal-Congo varies between 22 and 26,5 rows. The number of belly rows from animals from interior-Congo varies between 21,5 and 23 transverse rows. Note that the single COAST individual with 26,5 rows of collar-vent scales was asymmetrical, and that it actually had 27 rows on one side (either the left or the right) of its belly. Similarly, note that the single C-V count of 21,5 rows implies that either its left-side or its right-side exhibited only 21 rows (detailed below).

In the collar-vent count, low numbers (C-V = 22 or 23) occur in numerous COAST localities, and also occur in the INTERIOR area. The C-V count of the specimen from the Ubangi River drainage in the interior zone of Congo-Brazzaville (Likouala) has an average of 21,5 rows (22 left, 21 right), which is the lowest result in this 2006-2007 sample. In contrast, high numbers (C-V = 27 or 28) occur exclusively in animals from COAST countries. Since the sample of animals from INTERIOR localities is very small (three animals), it clearly remains possible that high collar-vent numbers can occur in the inland region of equatorial Atlantic-drainage Africa.

As earlier mentioned, these results about the collar-vent count can also to be tested for correlation with sex. The sex-variation hypothesis is tested in Table 4.5 (below) on specimens from Cameroon. In some additional tables (further below) the hypothesis will be tested on animals from other African nations represented in this relevant (n=47 total with C-V data) sample of *Osteolaemus tetraspis* Cope.

It is also a surprise that the collar-vent results in this thesis clearly falsify the Brazaitis (1973:79) hypothesis that *Osteolaemus tetraspis osborni* (the INTERIOR subspecies) has 21 to 23 transverse rows on its belly, compared with 26 to 27 C-V rows in the COAST taxon (*O. t. tetraspis*). Further, the apparent gap of separation between the two hypothetical (but C.I.T.E.S. recognized) groups of African dwarf-crocodiles appears now (with a larger sample) to not exist. In other words, there were no specimens with 24 or 25 collar-vent rows in the American sample in the early 1970's, but the Zoer 2006-2007 results include both 24 and 25 as observed.

Although the total sample reported in this chapter (n=47 for ventral characters) is large, the number of INTERIOR African dwarf-crocodiles is small (n=3). Interestingly, all three (= 100% of this subsample) INTERIOR animals agree with the Brazaitis (1973:79) prediction about *Osteolaemus tetraspis osborni* (Schmidt) having 21 to 23 collar-vent rows. Thus, it is the COAST subspecies (*O. t. tetraspis* which should have 26 to 27 C-V's) that violates the Brazaitis (1973) prediction.

Table 4.5 Frequency of collar-vent results from Cameroon possibly correlated with sex

Locality and subspecies	C-V	frequency	sex
Yaoundé & Campo Maan = COAST	22	3 out of 30	A
Yaoundé & Campo Maan = COAST	22,5	3 out of 30	B
Mundemba, Yaoundé, and Campo Maan = COAST	23	3 out of 30	C
Yaoundé & Mundemba = COAST	23,5	3 out of 30	D
Yaoundé = COAST	24	3 out of 30	no data
Yaoundé & Campo Maan = COAST	24,5	4 out of 30	E
Yaoundé = COAST	25	3 out of 30	no data
Yaoundé = COAST	25,5	2 out of 30	F
Campo Maan = COAST	26	1 out of 30	no data
Mundemba & Campo Maan = COAST	26,5	3 out of 30	G
Yaoundé = COAST	27	1 out of 30	male
Yaoundé = COAST	27,5	1 out of 30	female

The C-V count was recorded on thirty (30) African dwarf-crocodiles from Cameroon, as follows: A = XXL-161 female, #162 male, #173 male; and B = #156 no-sex, 164 no-sex, 169 male; and C = #167 female, 175 female, 183 male; and D = #150 no-sex, 166 female, 182 female; and E = #s 151, 153, 163 all with no-sex and # 172 female; and F = #159 no-sex and 174 female; and G = #160, 165 and 184 all male. In the sex column, the letters represent the following groups: A = 3 with sex from Cameroon (2 males, 1 female); B = 1 additional Cameroon with sex (male); C = 3 further additional Cameroon with sex data (1 male, 2 females); D = 2 more Cameroon specimens with sex (both female); E = 1 more with sex (female); F = 1 more female with sex known; and G = 3 more *Osteolaemus* with sex data (all males) from Cameroon nation. Note that the single female with 27,5 collar-vent rows had 28 (twenty-eight) C-V's on one side of its belly (counted the parallel way).

In Table 4.5 (above) sixteen African dwarf-crocodiles have sex data; and, of them, eight animals are male, and the same number of crocodiles are female. The ratio between males and females is also equally represented in the number of belly rows located between the gular collar and the cloacal-vent (the C-V character). Now, seeking better correlation in other nations, and across the subspecies boundary, further testing of the sex-variation hypothesis will next be presented, starting with specimens from Gabon in Table 4.6 (below). Note that in Cameroon, the highest collar-vent number (27,5 rows) occurred on a female, while the lowest number of C-V rows (22) was also observed on a different female (field number XXL-161), and also on males.

Table 4.6 Individual collar-vent results from Gabon possibly correlated with sex

XXL specimen #	locality detail and geographic-kind	C-V	sex
#130	Kango = COAST subspecies	25	female
#132	Kango = COAST subspecies	24	male
#134	Setté Cama = COAST subspecies	24,5	female
#135	Setté Cama = COAST subspecies	25	female
#136	Setté Cama = COAST subspecies	28	male
#137	Setté Cama = COAST subspecies	25,5	male
#138	Setté Cama = COAST subspecies	23,5	female
#139	Gamba = COAST subspecies	25	no data

The eight *Osteolaemus* in Table 4.6 from Gabon with data on collar-vent (C-V) row-counts are presented with their sex-data in this table. Seven out of eight African dwarf-crocodiles from Gabon have sex-data, and of them three are male, and four are female. The Gamba specimen (#139) has no data about its sex.

In this case the low of 23,5 is a female, and the high of 28 is a male, but 24 can be male or female; and, also 25 can be either sex. Again both sexes are almost equally represented. Finally, the collar-vent count in animals from Congo-Brazzaville and Zaïre-DRC has its sex-data presented. The sex-variation hypothesis for both COAST and INTERIOR animals will now be tested in Table 4.7 (below).

Table 4.7 Individual collar-vent results from Congo-Brazzaville and Zaïre-DRC possibly correlated with sex

XXL#	locality detail	nation	C-V	sex
#106	Bellelo = COAST	Congo-Brazzaville	25	female
#107	Bellelo = COAST	Congo-Brazzaville	26,5	female
#108	Bellelo = COAST	Congo-Brazzaville	22	male
#109	Bellelo = COAST	Congo-Brazzaville	25	male
#124	Youbi = COAST	Congo-Brazzaville	26	male
#125	Dembouanou = COAST	Congo-Brazzaville	26	male
--- --- ---	--- --- ---	--- --- --- --- --- ---	--- ---	--- --- ---
XXL#	locality detail	nation	C-V	sex
#111	Likouala = INTERIOR	Congo-Brazzaville	21,5	male
#118	Likouala = INTERIOR	Congo-Brazzaville	23	male
--- --- ---	--- --- ---	--- --- --- --- --- ---	--- ---	--- --- ---
#17	Kinshasa = INTERIOR	Zaïre-DRC	22	female

Six African dwarf-crocodiles from coastal-Congo with sex data are in this case four males and two females. Additionally, three animals with sex data from interior-Congo are two males from Congo-Brazzaville at Likouala River (#111 and #118) and one female (#17) from Zaïre-DRC at Kinshasa. Note that a collar-vent count of both 25 and 26 C-V's occurs in both sexes. The same goes for low numbers in the C-V count (=22 or 23 transverse scale rows from the gular collar to the cloaca). The high in this table is 26,5 on a female, but 26 occurs also on males. The low in this table is 21,5 on a male, but 22 occurs on a female in the same INTERIOR hypothetical taxon.

The sex of the African dwarf-crocodile appears to have little or no influence on the number of transverse rows between the gular collar and the cloacal oval (vent). The second character of the belly to be tested is the number of transverse scales across the widest part of the belly of an African dwarf-crocodile. The number of transverse scales on the belly is counted in the 8th, 9th and 10th row from the gular collar. These three transverse rows were observed to satisfactorily answer the description of being the widest level across the

Osteolaemus belly (n=47). In other words, no specimens of African dwarf-crocodiles in the Zoer 2006-2007 sample exhibited reason to deviate from these three selected rows in an effort to record the widest (longest transverse) level across the belly as the ninth (9th) row, and its immediate neighbours. The results about this belly character are presented in Subsection 4.3.2, below.

4.3.2 Number of scales across the widest part of the belly

The second count, the maximum number of scales in a transverse belly row, was recorded on the same 47 African dwarf-crocodiles that were described in Subsection 4.3.1 (above). The number of scales in the selected three designated transverse belly rows, without concern about geographic and-or sexual variation, is displayed in Table 4.8, below.

Table 4.8 Number of scales in the 8th, 9th, and 10th transverse row from the gular collar (n=47)

# scales	frequency row 8	frequency row 9	frequency row 10
Eight scales	0 out of 47	2 out of 47	3 out of 47
Nine scales	1 out of 47	1 out of 47	7 out of 47
Ten scales	12 out of 47	10 out of 47	12 out of 47
Eleven scales	22 out of 47	18 out of 47	13 out of 47
Twelve scales	8 out of 47	13 out of 47	12 out of 47
Thirteen scales	4 out of 47	2 out of 47	0 out of 47
Fourteen scales	0 out of 47	1 out of 47	0 out of 47

All three of the designated transverse rows across the widest part of the belly show similar results. The majority of the 47 African dwarf-crocodiles have ten, eleven or twelve scales in a qualifying row across the belly. Eleven scales in a transverse row is the most common outcome in all three rows individually, and thus also collectively (as tabled below).

In Table 4.8 (above) the number of scales is presented by the transverse-row number, calculated by counting away from the gular collar (= posteriorly). To get a total view, the results of all three of the widest rows on the belly (8th, 9th and 10th rows below the gular collar) are lumped together. The results, in numbers and in percentages, (n=141, meaning n=47x3) are presented in Table 4.9, below.

Table 4.9 Total number of scales in three transverse rows across the belly, when the results of the 8th, 9th, and 10th rows are all lumped together (n=141)

Number of scales in row	total frequency	percentage
Eight (8) scales	5 out of 141	3,5 %
Nine (9) scales	9 out of 141	6,4 %
Ten (10) scales	34 out of 141	24,1 %
Eleven (11) scales	53 out of 141	37,6 %
Twelve (12) scales	33 out of 141	23,4 %
Thirteen (13) scales	6 out of 141	4,3 %
Fourteen (14) scales	1 out of 141	0,7 %

The maximum number of scales in a transverse row across the widest level of the belly varies between eight and fourteen. Fifty-three of the transverse rows reported in this table have eleven scales in it, which corresponds to a percentage of 37,6 %. Ten and twelve transverse scales are almost equally represented as totals in this sample of mid-belly maximum numbers of proper “ventral” scales.

The Charette (1995:orange 9) prediction is 10 to 12 ventral-scales across the belly in the COAST subspecies, compared with 12 to 14 across in *Osteolaemus tetraspis osborni* (Schmidt) in the INTERIOR. Both Fuchs (1974:168, 172) and Fuchs (2006:133, 136) agree with the C.I.T.E.S. numbers about this character, but King + Brazaitis (1971:26) and Brazaitis (1973:79) declined the temptation to publish data about this character in a comparison including all of the known living crocodilian taxa. Thus, the literature is three publications, and the sample size is unknown, and the locality data is suspect because this remaining literature sample of *Osteolaemus t. tetraspis* and *O. t. osborni* was based by Fuchs (1974, 2006) on commercial skins (mostly in Germany) that have not been deposited in museums.

According to the Charette (1995) C.I.T.E.S. guide, the maximum (highest) number of ventral scales along the transverse mid-level across the widest (broadest) part of the belly should be fourteen (14), and the Zoer 2006-2007 sample of n=47 *Osteolaemus tetraspis* agrees with C.I.T.E.S. about this detail, though the frequency of the number 14’s occurrence in the new data is remarkably low. In contrast to the maximum (high), the predicted minimum (low) result for this character was ten (10) ventral scales across the widest belly.

Note that the data in the preceding table has extended the lower limit in this character to include nine (9) scales, and also eight (8) scales within this species. Thus, the number of ventral scales across the widest midbody in the African dwarf-crocodile is now newly known to vary from eight (8) to fourteen (14), and this variation is apparently not significantly influenced by the sex of the animal.

In the remaining part of this chapter, the results about the belly scales will be discussed by country. The sex-variation hypothesis is also tested in this next part as another possibility for correlating this second transverse belly-scale character with biology. The data for specimens from Congo-Brazzaville and Zaïre-DRC are presented in Table 4.10, below, and other nations will follow.

Table 4.10 Number of scales across the widest part of the belly on specimens from Congo-Brazzaville and Zaïre-DRC, with notes about sex

XXL #	locality detail	8th row	9th row	10th row	sex
#106	Bellelo = COAST	11	11	10	female
#107	Bellelo = COAST	12	12	12	female
#108	Bellelo = COAST	12	11	10	male
#109	Bellelo = COAST	13	12	12	male
#124	Youbi = COAST	12	10	10	male
#125	Dembouanou = COAST	11	11	11	male
---	---	---	---	---	---
XXL #	locality detail	8th row	9th row	10th row	sex
#111	Likouala = INTERIOR	11	12	12	male
#118	Likouala = INTERIOR	11	12	12	male
---	---	---	---	---	---
#17	Kinshasa = INTERIOR	11	11	11	female

The individual specimens with ventral data from coastal Congo, and interior Congo and Zaïre-DRC commonly exhibit 11 or 12 belly scales in a transverse row; and, both sexes can have any of the four observed outcomes (*ie*., 13, 12, 11 or 10 scales). All COAST localities are *Osteolaemus tetraspis tetraspis* Cope, while the two INTERIOR locations are the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies.

There is little difference in the number of transverse scales across the widest part of the belly between male and female specimens, and also between the COAST localities and the two INTERIOR locations in this sample. Two additional coast localities are Gabon and Cameroon nation. The detailed data for the eight African dwarf-crocodiles examined in Gabon are presented and analysed in Table 4.11, below.

Table 4.11 Number of scales across the widest part of the belly of specimens from Gabon (n=8), with notes about sex

XXL #	locality detail	8th row	9th row	10th row	sex
#130	Kango = COAST	10	10	9	female
#132	Kango = COAST	13	11	10	male
#134	Setté Cama = COAST	11	10	10	female
#135	Setté Cama = COAST	11	11	10	female
#136	Setté Cama = COAST	11	13	10	male
#137	Setté Cama = COAST	10	9	8	male
#138	Setté Cama = COAST	13	14	12	female
#139	Gamba = COAST	10	10	11	no data

The number of scales in a transverse belly-row in Gabon animals varies between eight and fourteen scales. Three specimens are male, four are female, and one has no data about its sex. All COAST localities are *Osteolaemus tetraspis tetraspis* Cope, while the two INTERIOR locations are the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies.

The average number of ventral-scales across the widest part of the belly in animals from Gabon is lower than the average of belly scales in the table before it (= Congo-Brazzaville and Zaïre-DRC animals). In other words, specimens from Congo-Brazzaville and Zaïre-DRC did not exhibit nine (9) or eight (8), but these low numbers, and also many number ten (10) results, are now known to occur in Gabon. The difference between Gabon and the two Congo’s (Congo-B and Zaïre-DRC) appears to not be caused by sexual variation, but could possibly correlate with geography (Gabon is an entirely COAST nation according to C.I.T.E.S.). The third coastal locality with data on belly scales is Cameroon. In this case, the results are presented in a slightly different format, because of the higher number of specimens from the coastal localities in Cameroon. The specimens from any given locality that have the same maximum number of scales in a transverse row across the belly are lumped together into groups that are then displayed in Table 4.12, below.

Table 4.12 Number of scales across the widest part of the belly of specimens from Cameroon (n=30), sex-data examined

Locality detail and geographic-kind	transverse scales	frequency	sex
Yaoundé = COAST	8 - 9 scales	1 out of 30	female
Yaoundé = COAST	9 - 11 scales	1 out of 30	no data
Yaoundé = COAST	9 - 12 scales	1 out of 30	no data
Yaoundé = COAST	10 - 12 scales	15 out of 30	A
Yaoundé = COAST	12 - 13 scales	1 out of 30	no data
--- --- --- --- --- --- --- --- ---	--- --- --- --- ---	--- --- ---	--- ---
Mundemba = COAST	9 - 11 scales	2 out of 30	B
Mundemba = COAST	10 - 12 scales	1 out of 30	male
--- --- --- --- --- --- --- --- ---	--- --- --- --- ---	--- --- ---	--- ---
Campo Maan = COAST	8 - 10 scales	2 out of 30	C
Campo Maan = COAST	9 - 11 scales	1 out of 30	female
Campo Maan = COAST	10 - 12 scales	4 out of 30	D
Campo Maan = COAST	11 - 13 scales	1 out of 30	no data

Fifteen animals from Cameroon at Yaoundé have ten, eleven or twelve transverse belly scales in a transverse row, when results from the 8th, 9th and 10th rows posterior to the gular collar are examined together. The same applies to the single male at Mundemba, and also to the four specimens (D) at Campo Maan.

Letters in the sex column of Table 4.12 (above) mean: A = XXL-148-153, #156, and #159 all with no-sex, #s166-167 females, #s169-170 males, #171 female, #173 male, #174 female; and B = XXL-182 female and #184 male; and C = XXL-161 female and #162 male; and D = XXL-160 male and #s 163-164 no-sex, and #165 male. The *Osteolaemus tetraspis* sex data (when known) appears to be random about correlating sex with the number of scales in a transverse row. There are three single animals with sex data in Table 4.12 (one male and two females). In addition there are four groups represented by letters, as follows: A = 7 with sex from Yaoundé (3 males, 4 females); B = 2 with sex from Mundemba (1 male, 1 female); C = 2 with sex from Campo Maan (1 male, 1 female); and D = 2 more Campo Maan with sex (2 males).

In the preceding table, because the Charette (1995) current C.I.T.E.S. distribution of *Osteolaemus tetraspis* subspecies places all of the nation of Cameroon in the COAST category, the C.I.T.E.S. prediction of ten to twelve (10-12) ventral scales across the widest transverse level of the belly was expected to always apply. Indeed it applies frequently, but not always, because fewer scales (8-9) can be expected to occur in Cameroon, and very rarely thirteen (13) ventrals can happen.

In Tables 4.2 to 4.7 (above), the collar-vent count was discussed country by country. Now, though, in order to compare the COAST data with the INTERIOR results from the collar-vent counts in total, all of the countries that have belly-count results (= data) are lumped together, and are then presented (in C.I.T.E.S. taxonomic summary) in Table 4.13 below.

Table 4.13 The collar-vent (C-V) count, COAST versus INTERIOR

Nation and geographic-kind	*Osteolaemus* subspecies	C-V count =
Cameroon = COAST (n=30)	*O. tetraspis tetraspis*	22 – 27,5
Gabon = COAST (n=8)	*O. tetraspis tetraspis*	23,5 – 28
Congo-Brazzaville = COAST (n=6)	*O. tetraspis tetraspis*	22 – 26,5
Nation and geographic-kind	*Osteolaemus* subspecies	C-V count =
Congo-Brazzaville = INTERIOR (n=2)	*O. tetraspis osborni* (Schmidt)	21,5 – 23
Zaïre-DRC = INTERIOR (n=1)	*O. tetraspis osborni* (Schmidt)	22

The range of variation in the collar-vent count on the belly on animals from near the Atlantic coast (n=44) is 22 – 28 rows, while in contrast the range of variation in C-V count in the continental interior of Africa (n=3) is 21,5 – 23 belly rows. Note that this INTERIOR result could be caused by small sample size.

In coastal animals, and also in animals from the inland interior of Africa, low numbers in the collar-vent character can occur. However, in African dwarf-crocodiles from localities near the Atlantic coast, higher numbers in the C-V count can also occur; while, in contrast, the inland animals all lack high numbers (when n=3).

Among the three INTERIOR examples of the theoretical (= geographically determined to taxon) *Osteolaemus tetraspis osborni* (Schmidt), one individual specimen exhibited only twenty-one (21) collar-vent rows, and notably only on one side of its belly. Thus, in this asymmetrical individual it was correctly predicted by Brazaitis (1973:79) that when twenty-one C-V rows occurs, it will only be in the *O. t. osborni* subspecies. However, it was also predicted (all sources) that twenty-two and twenty-three rows would also be exclusively restricted to INTERIOR localities, but that conclusion (from the literature) is not supported by the Zoer 2006-2007 expedition's data.

The relevant data in the Charette (1995:orange 9) guide, and also in Fuchs (1974:168, 172) and Fuchs (2006:133, 136), all indicates that all of the COAST animals should have 25 to 29 C-V rows. However, and surprisingly (because this new data is not dominated by siblings), the C.I.T.E.S. prediction is falsified by the n=47 data from the 2006-2007 Zoer expedition. It is newly established that many individual animals in the *Osteolaemus tetraspis tetraspis* hypothetically necessary subspecies (as defined by C.I.T.E.S. geography) exhibit fewer than twenty-five (25) transverse rows of ventral scales in their collar-vent longitudinal row-count character (counted the parallel way). Thus, the predicted possible discrepancy between counting along the midline, as opposed to parallel to it, should (or could) sometimes yield higher midline numbers, but the relatively low (small) C-V counts of twenty-two (22) and twenty-three (23) in the COAST group can not necessarily be entirely explained-away by this postulated methodological difference.

The C.I.T.E.S. collar-vent prediction (in the Charette guide, and also in both of the Karlheinz Fuchs books) is falsified by this new and world-record size sample from the Zoer 2006-2007 *Osteolaemus* expedition. Now, it is clear that many COAST (*O. t. tetraspis*) dwarf-crocodiles can be correctly identified by their collar-vent (C-V) numbers, but not all of them. The collar-vent character is not predictive 100% of the time. Similarly, all *Osteolaemus tetraspis osborni* can exhibit the predicted number of C-V rows, but some of the COAST animals also exhibit the INTERIOR subspecies condition.

In another attempt to achieve separation between the two C.I.T.E.S. subspecies, the number of transverse scales across the widest part of the belly from the coastal animals is compared with the inland animals, as presented and analysed in Table 4.14 below.

Table 4.14 Scale counts across the widest part of the belly, COAST versus INTERIOR

Nation and # specimens	geographic-kind and subspecies	across belly count
Cameroon (n=30)	COAST = *O. tetraspis tetraspis*	8 – 13 scales
Gabon (n=8)	COAST = *O. tetraspis tetraspis*	8 – 14 scales
Congo-Brazzaville (n=6)	COAST = *O. tetraspis tetraspis*	10 – 13 scales
Nation and # specimens	geographic-kind and subspecies	across belly count
Congo-Brazzaville (n=2)	INTERIOR = *O. tetraspis osborni*	11 – 12 scales
Zaïre-DRC (n=1)	INTERIOR = *O. tetraspis osborni*	11 scales

The range of variation in the number of scales across the widest part of the belly of African dwarf-crocodiles from localities near the Atlantic coast (n=44) is 8-14 scales across, while in contrast the range of variation in scales across the widest part of the belly in animals from the interior of equatorial continental Africa (n=3) is 11-12 scales.

In the Zoer 2006-2007 expedition’s sample of forty-seven (47) African dwarf-crocodiles with known ventral scalation data, the largest (= highest, and maximum) number of ventral scales in a transverse row crossing the widest part of the belly is fourteen (14). This outcome was predicted by all three of the published reports of data about this ventral scalation character. In other words, Karlheinz Fuchs (1974:168, 172) said that the range of variation in *Osteolaemus tetraspis* as a species is 10 to 14, and Charette (1995:orange 9) said that there can be ten to fourteen (10-14) across the belly at its widest transverse level; and, later Fuchs (2006:133, 136) agreed with his earlier numbers, and also with the exact same range of variation in C.I.T.E.S. (Charette, 1995:orange 9).

The prediction in the various repetitions of the 10 to 14 range of outcomes, when counting across the widest (= broadest, and longest) level of the belly, was that fourteen (14 true ventrals across mid-belly level) would only occur in the INTERIOR subspecies (*Osteolaemus tetraspis osborni*). Similarly, it was earlier predicted that thirteen (13) of these ventral scales would occur only in the *O. t. osborni* subspecies. Both of these two predictions are falsified by the n=47 sample in this thesis, because COAST specimens of the alternative subspecies (*O. t. tetraspis* as geographically defined by C.I.T.E.S.) is the one and only relevant taxon that exhibits 13 and 14 in Gabon, and thirteen (13 ventrals across at mid-belly) occurs additionally in Cameroon, and in the coastal part of Congo-Brazzaville.

The "across-the-belly" ventral scale-count prediction from the three existing publications was that low numbers (as results for this character) occur only on COAST animals; and, in contrast (but with minor overlap), high numbers are restricted to the INTERIOR. Thus, *Osteolaemus tetraspis tetraspis* was allowed 10 to 12, while *O. t. osborni* had 12 to 14 ventral scales across its widest mid-belly level.

Aside from the weakness in the Charette (1995:orange 9) definitions that twelve (12) ventral scales across the mid-belly can occur in both taxa, the Zoer 2006-2007 sample (n=47) of African dwarf-crocodiles contradicts the C.I.T.E.S. prediction, and further suggests that it is backwards. In other words, low counts in this transverse character appear to occur in the INTERIOR (n=3), compared with high counts (numbers like 13 and 14), which are now known to characterize the COAST taxon (n=44) incompletely, because extremely low results (such as 8 or 9) can occur in *O. t. tetraspis* near the Atlantic, meaning that the COAST category includes both low and high numerical extremes for this character (the second kind of ventral scalation count in this chapter).

Finally in a combined overview, the lack of predictiveness that is known to characterize these two standard kinds of ventral scalation characters on the belly of the African dwarf-crocodile is disappointing for C.I.T.E.S., and thus also for many crocodilian conservation and protection efforts in the equatorial African region. Further, it has been shown, in Chapter 2 and in Chapter 3, that the two major kinds of scales on the dorsal surface of the neck (= the PO's, and the nuchals) in *Osteolaemus tetraspis* as a species are similarly not 100% predictive about which of the two C.I.T.E.S. subspecies is represented. Therefore, it is necessary to examine a series of additional "standard" (though often subject to slightly different and-or vague definitions) dorsal scalation characters (the pelvis, the proximal half of the tail, and the proper body of the African dwarf-crocodile), beginning with Chapter 5, below.

4.4 REVIEWING THE TWO KINDS OF VENTRAL SCALATION CHARACTERS

The 2006-2007 expedition's data about the two kinds of C.I.T.E.S. belly scalation characters (n=47 *Osteolaemus*) was found to contradict the C.I.T.E.S. hypothesis that longitudinal counts of the number of transverse C-V rows, and also transverse counts of the number of individual ventral scales in the widest mid-body row(s), are predictive about which of the two *Osteolaemus tetraspis* subspecies is represented by any animal. With both subspecies present in the 2006-2007 *Osteolaemus* sample, it is now newly known that it is generally true that 100% certain taxonomic identification is possible only in a relatively few and rare cases of low extremes in observed variation in C-V numbers. The same is true about the ventral scale-count across the widest mid-belly level. Thus, neither of these two independent kinds of belly-skin characters are guaranteed to identify all *Osteolaemus tetraspis* specimens to the correct subspecies taxon 100% of the time. Rather, the C.I.T.E.S. belly-skin characters can sometimes give (with apparent confidence) the wrong taxonomic results.

In a summary format, the two kinds of ventral scale counts, that in some cases were formerly thought to be diagnostic in *Osteolaemus tetraspis* at the subspecies level, are reviewed as a list of literature citations in Table 4.15 (below).

Table 4.15 Literature data about ventral scale-counts in African dwarf-crocodiles

Paper	taxon	C-V rows	scales across
Fuchs 1974	COAST	25 to 29	10 to 12
Fuchs 2006	COAST	25 to 29	10 to 12
Charette 1995	COAST	25 to 29	10 to 12
Charette 1995	INTERIOR	22 to 24	12 to 14
Fuchs 2006	INTERIOR	22 to 24	12 to 14
Fuchs 1974	INTERIOR	22 to 24	12 to 14
Brazaitis 1973	INTERIOR	21 to 23	no data
Brazaitis 1973	COAST	26 to 27	no data
King + Brazaitis 1971	COAST	21 to 27	no data
King + Brazaitis 1971	INTERIOR	21 to 27	no data

To make it a little easier to see the COAST and INTERIOR geographic categories (the two subspecies), the papers cited it this table are each listed twice. The “C-V rows” character is the number of transverse rows of belly scales between the pectoral collar and the cloacal oval. The “scales across” character is the number of ventral scales in the transverse row at the widest level across the belly.

As a species, the literature prediction for the two *Osteolaemus tetraspis* ventral scalation characters is 21-29 C-V rows, and 10-14 ventral scales in the row(s) across the widest level of the belly. These numbers are the limits of variation in the character’s results in the African dwarf-crocodile (from published papers), and the same group of papers are cited for their limits of variation in these two characters in comparison with the ranges of variation newly recorded in the 2006-2007 sample of *Osteolaemus tetraspis* with both subspecies combined as one dwarf-crocodile species in Table 4.16 (below).

Table 4.16 Ranges of ventral-scalation variation from the literature, compared to this field-work sample

Paper(s)	C-V rows	scales across
K. Fuchs (1974, 2006)	22 to 29	10 to 14
Charette (1995)	22 to 29	10 to 14
King + Brazaitis (1971) and Brazaitis (1973)	21 to 27	no data
The 2006-2007 sample	21,5 to 28	8 to 14

The total range of variation in the Zoer 2006-2007 expedition's data for these two kinds of ventral scalation characters is a fairly good fit with the earlier published predictions. Note that with the C-V counts made the parallel way in the new sample, the 21,5 C-V rows result implies that one side had 21,0 rows, while the other side had 22,0 collar-vent rows. Also note that the published results of 29 C-V scales along the ventral midline could include an insignificant midline anomaly that would be avoided by the parallel method employed in this thesis.

Although several tempting but minor taxonomic coincidences occur in both of the ventral scalation characters, these correlations with subspecies taxa are always at the extremes of variation in the relevant character. Thus, even if real (as opposed to being an artifact of small sample size), these special cases still fail to identify the vast majority of specimens as being one subspecies or the other.

CHAPTER V SEVERAL WAYS TO SEPARATE THE BODY FROM THE TAIL

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

5.1 INTRODUCTION

While the preceding chapters were visual characters that did not require any physical handling of actual living or dead African dwarf-crocodiles, the subject here in Chapter 5 involves hands-on examination and manually feeling the bones of the crocodile's skeleton with human finger tips. The publication by Franklin D. Ross and Gregory C. Mayer (1983: Museum of Comparative Zoology, Harvard University) in Annexure A (below) becomes important in Chapter 5, and Ross + Mayer (1983) continues to be crucially and centrally involved in Chapters 6 and 7, and to a lesser degree Chapter 8 also.

The scale counts that were discussed in Chapter 2 (the post-occipitals), and in Chapter 3 (the nuchals), and in Chapter 4 (the collar-vent count and the number of transverse scales across the widest part of the belly), are all externally visible characters. It has been shown in Chapters 2 and 3 that the dorsal-armour scales on the neck of the African dwarf-crocodile can usually be analysed from photographs of the cervical region that show the posterior edge of the head, and that also include the anterior several rows of the thoracic armour series that are closest to the base of the crocodile's neck.

For ventral scale-counts, it has also been mentioned that photographs of the crocodilian belly, to be useful for the purpose of counting the number of transverse rows between the throat collar (see above in Figure 4.1) and the cloacal-vent disturbance (see above in Figure 4.2), must include the ventral "gular collar" scales located in the pectoral region between the front legs (the crocodile's arms), and must also include at least the anterior end of the ventral cloacal zone, located roughly close to, and slightly caudally (toward the tail) in relation to the ventral skin located between the two back legs, at the posterior end of the count of collar-vent belly-rows (see Chapter 4, above). It is theoretically possible to record the belly-scales data (patterns and numbers) for later analysis by physically placing small crocodiles directly on top of a photocopy machine that is protected by a thin and clear sheet of transparent plastic. However, all of the data reported in Section 4.3 was taken (as numbers) directly from physical dwarf-crocodiles in the field, and was sometimes supplemented and clarified with drawings and photographs.

One significant Ross + Mayer (1983) assertion, about the transverse rows of ventral scales in the collar-vent (C-V) belly count not being correlated in any way with the bones of the vertebral column, was noted above in Chapter 4 (the CV count). However, Ross + Mayer (1983:fig. 11) also showed that on the crocodilian tail, those ventral transverse rows that are posterior to the cloacal disturbance zone are normally correlated in the same one-to-one relationship with their associated (in this case "overlying") vertebrae that exists between transverse dorsal scale-rows and their underlying (and very slightly offset) vertebrae in the dorsal-armour precaudal series PC-1 to PC-18 on the crocodilian body. The precaudal (PC-1 to PC-18 on the body) and the caudal (C-1 to the posterior tip of the tail) numbering systems are explained here in Chapter 5 as being dependent on the accurate determination of the sacro-caudal juncture (SC-J), and this centrally important dorsal-armour character is illustrated in Figure 5.1.

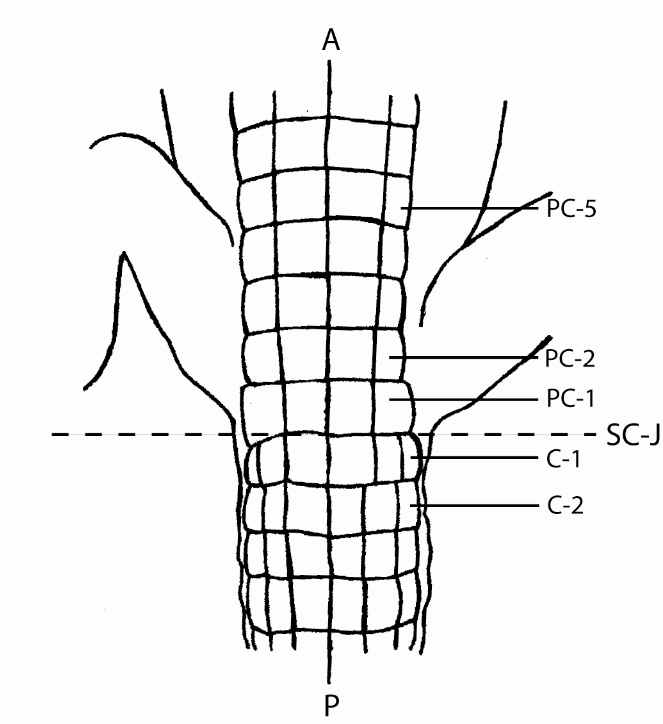


Figure 5.1 The sacro-caudal juncture (SC-J) is a transverse line dividing the precaudal zone from the caudal zone

The sacro-caudal division line occurs between two rows of dorsal scales (PC-1 and C-1), making those anterior to it become precaudals (PC-1 to PC-18 going toward the neck), and causing those that are posterior to the SC-J line to become transverse rows of dorsal caudal scales (C-1 to the tip of the tail). This male specimen (XXL-124), *Osteolaemus tetraspis* Cope, from Congo-Brazzaville COAST at Youbi, is 62,25 cm in length.

Transverse rows of dorsal armour scales are numbered in the Ross + Mayer (1983:308-311) model as two separate series. Starting at the sacro-caudal juncture (SC-J), and going anteriorly (through the sacral and lumbar and thoracic regions) toward the neck and the crocodile's head is the precaudal group of eighteen transverse rows on the body (PC-1 to PC-18). Similarly, but progressing in the opposite direction, the dorsal armour caudal group is numbered posteriorly from the SC-J level, first with caudal one (C-1), and then advancing toward the tip of the tail. Thus, C-3 (the third caudal row) is the third tail-crossing scale-row located posterior to the transverse line of sacro-caudal division (SC-J) between the pelvis and the tail. In the proximal part of the tail (the basi-caudal region), the transverse rows of dorsal-armour scales are relatively flat across the dorsal surface, and this subset of the tail is discussed as "double-crested caudals" in Chapter 6 (below). The distal series of tail rows that have a single knifelike scale on the dorsal surface are the "single-crest caudals" which are of relatively little scientific worth on commercial size *Osteolaemus* as a scale count, because the tip of the tail is very often damaged.

Looking ahead, the scale counts that will be discussed in Chapter 6 (double-crested caudals), and also in Chapter 7 (precaudals 1-18 on the body), will completely depend on finding the accurate location of the transverse line between two special rows at the sacro-caudal juncture (SC-J) which delimits the posterior end of the crocodile's body, and is the level at which its true tail (caudal segment) begins. The dorsal sacro-caudal juncture is immediately posterior to the animal's pelvis, but on the crocodilian belly-skin the dorsal SC-J is not present, though in theory it would always be located considerably anterior to the ventral start of the tail, which is currently defined by C.I.T.E.S. (1995 identification guide from Charette) as the first transverse row to pass posterior to the cloacal obstruction (see Section 5.3, below).

Because the Ross + Mayer (1983:fig. 11-B) illustration shows the first postcloacal transverse row of scales to be the third caudal row (C-3) on an *Osteolaemus tetraspis* Cope specimen, that condition is arbitrarily adopted here for the African dwarf-crocodile, below, in Section 5.3, as the tested hypothesis for the most anterior post-cloacal "whorl" (transverse row of contiguous scales). In other words, because the hypothetical test prediction in this thesis is for caudal-row number three (C-3) to be constant, any results other than C-3 will falsify the simplified assertion. This will be a case of a dorsal-ventral skin correlation working 100% of the time (very useful to science), or not (= it remains a variable). In addition to the ventral scalation character (to be further discussed in Subsection 5.3.3, below), there are also two dorsal-view hypotheses tested before it (in Subsections 5.3.1 and 5.3.2), and all three of these questions discussed here in Chapter 5 are potential variables that completely rely on the accurate location of the sacro-caudal juncture (SC-J) being known.

5.2 METHODS

The Ross + Mayer (1983) technique for locating the sacro-caudal juncture (SC-J) involves locating precaudal transverse-row number one (PC-1) by a weighted combination of three independent methods, of which the third method (Ross + Mayer's "criterion three") is a possible variable, but for which the first two criteria were already proven in 1983 as being reliable. Further, Ross + Mayer (1983:308) maintained that their criterion one (physically feeling the posterior edges of the iliac crest of the crocodilian pelvis) is usually sufficient. However, the Ross + Mayer (Cambridge, Mass., USA) paper also offered criterion two (outstretched femurs) as a double-check, and as an additional factor to be considered in any cases of ambiguity in the results of criterion one (the iliac crest).

The questions presented in the field protocol, about successfully locating the sacro-caudal juncture (SC-J), were answered in a specific order. The questions about the three independent methods were:

- Can the SC-J be located successfully by physically feeling the posterior edges of the iliac crest of the crocodilian pelvis, yes or no? (= criterion one)
- Can the SC-J be located successfully by outstretching the femur bones, yes or no? (= criterion two)
- Can the SC-J be located successfully by variation in the width of the transverse dorsal rows, yes or no? (= criterion three)

5.3 RESULTS

Finding the first precaudal transverse row of dorsal scales by manually squeezing the crocodile's pelvic region (Ross + Mayer's criterion one) is the recommended method, and as will be shown in Table 5.1 (below), the iliac crest was the primary technique applied to the Zoer 2006-2007 African dwarf-crocodile sample, and it was usually sufficient for an unambiguous outcome, but in more than 50% of examinations of *Osteolaemus tetraspis* specimens, criterion two (outstretched femurs) was supplementarily recorded. The data in Table 5.1 does not necessarily reflect iliac-crest ambiguity (uncertainty about the results of criterion one is not even suggested), because the researchers were encouraged to test the reliability of criterion two when time was available, just for the theoretical fun and certainty of it. In other words, usually data-takers employed criterion two (the outstretched femur bones) when the results of criterion one (the posterior edges of the pelvis) were not at all ambiguous. The application of criterion two was double-checking.

Table 5.1 Sacro-caudal juncture found by combination of two skeleton-based criteria

Skeleton-based methods (Ross + Mayer, 1983)	# of dwarf-crocodiles
Criterion one (back-edges of iliac bones)	68 out of 68
Criterion two (outstretched femur bones)	49 out of 49 sampled

Criterion one (iliac bones) was successful in 100% of the possible cases in the Zoer 2006-2007 sample of *Osteolaemus tetraspis* Cope encountered and examined in five equatorial western African nations. Criterion two (femur bones) was successful 100% of the time in its (72% of 68 possible) smaller sample.

Thus, there was a high rate of success in finding the sacro-caudal juncture by both of the skeleton based methods (Ross + Mayer's criteria #one and #two). Details about finding the sacro-caudal juncture are presented below in Sections 5.3.1 to 5.3.3.

5.3.1 Sacro-caudal juncture by relative width confirms pelvis and femurs, yes or no?

The first of three methods being tested is from Ross + Mayer (1983), where it was presented as a visually available variable with a relatively high probability of being proved to be constant among many taxa of living crocodilians, but for which some exceptions are known. An example of this external visual character working (being affirmative) on an African dwarf-crocodile, *Osteolaemus tetraspis* Cope, is presented in Figure 5.2.

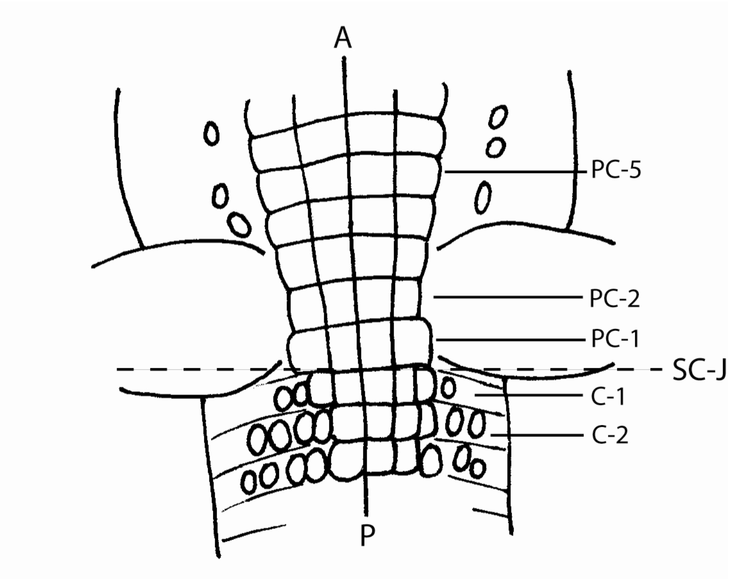


Figure 5.2 Transverse width of PC-1 compared with that of its neighboring transverse rows of dorsal armour in the lumbar (PC-3-5, etc.), pelvic (PC-1-2), and anterior caudal (C-1-2, etc.) zone

PC-1 is slightly wider-across than PC-2 is, but PC-3, 4, 5, etc. are wider than PC-2 is. The caudal dorsal scales and their subdorsal adjacent scales are often difficult to distinguish from each other. The caudal-row width across is thus not comparable to the width across in the sacral and lumbar, etc. regions. Ross + Mayer (1983:308) said that: “In many species, PC-1 is the first transverse row to become broader after monotonically decreasing in breadth from midbody towards the sacrum”. This male specimen (XXL-124), *Osteolaemus tetraspis* Cope, from Congo-Brazzaville COAST at Youbi illustrates the monotonic decreasing in breadth from PC-5 to PC-2.

If it is experimentally found that the width of PC-1 in comparison with the transverse width of the rows anterior to it (PC-2, PC-3, PC-4, etc.) is a reliable external indicator of the internal skeleton in *Osteolaemus tetraspis* Cope, it means that flat hornback trophy skins become accessible for analysis of the Ross + Mayer (1983) kind, because the sacro-caudal juncture (SC-J) can be reliably located. In addition, this applies to stuffed (taxidermied) African dwarf-crocodiles (tourist curios, museum exhibits and scientific study skins), and also to live examples of the species on public view behind barriers, at zoos, and farms.

If PC-1 and the sacro-caudal juncture can be consistently found by what Ross + Mayer (1983) called “criterion three” (relative width of PC-1), then selected photographs of living and dead *Osteolaemus* would become useful for several significant characters, including Chapters 6-7 (below).

The fortunate outcome of the experiment, to determine if width predicts and identifies the first precaudal row (PC-1) and the sacro-caudal juncture (SC-J) line, is documented in Table 5.2, in which results of the three Ross + Mayer (1983) criteria for finding PC-1 in *Osteolaemus tetraspis* are compared with each other for accuracy.

Table 5.2 Width confirms pelvis and femurs? Yes.

Methods of finding PC-1 and the SC-J	success rate
Criterion 1 (feeling the iliac crest = constant)	100% (n=68)
Criterion 2 (outstretched femurs = constant)	100% (n=49)
Criterion 3 (width of PC-1 = tested variable)	98,5% (n=68)

The results in Table 5.2 of the two skeleton-based methods (criteria 1 + 2) are confirmed by the relative transverse width (criterion 3). Criteria 1 + 2 above have a 100% rate of success. Criteria 3 has a 98,5% rate of success, because in one animal the width did not confirm pelvis and femurs. The Zoer 2006-2007 *Osteolaemus tetraspis* Cope sample is from five equatorial western African nations.

Ross + Mayer's (1983:308) prediction that the relative width of the first precaudal transverse row of dorsal armour scales (PC-1) could be reliably useful in some crocodilian taxa appears to be true in *Osteolaemus tetraspis* Cope on all but one individual in the group of examples examined from Congo-Brazzaville, Zaïre-DRC, Gabon, Cameroon, and Benin. Any absences of criterion 2 data from the 68 possible African dwarf-crocodiles was an artifact of fieldwork circumstances, and thus was randomly selected, and should not influence the result.

5.3.2 Posterior edge of back leg reliably locates S-C juncture, true or false?

If it reliably works on *Osteolaemus tetraspis* Cope, the back edge of the hind legs method of finding the first caudal row (C-1) on the African dwarf-crocodile will have, in addition to the usual benefits of a visually accessible character, the special bonus-value that scale-counts from the Zoer 2006-2007 African expedition can be directly compared with all of the already existing modern double-crested caudals (DCC) data in the published literature (see Dr. Robert Inger and also C.I.T.E.S. and others in Chapter 6, below).

Further, if the posterior edge of the hind limb is a constant in dwarf-crocodiles from the equatorial rain-forests of Africa, the results can be compared with the DCC numbers in other crocodilian species, if-and-where the back-legs technique has been proven to be consistent for reliably locating the base of the tail (transverse caudal row #1).

Some crocodilians have long and thin back legs (for example, *Tomistoma schlegelii*, the Malayan and Borneo false gavial), while other species such as *Osteolaemus tetraspis* have short and fat legs (Figures 5.2 above, and 5.3 below) with remarkably thick femur sections when the muscle and skin is present.

Although the transverse level of the back edges of the hind limbs has been the standard line dividing the crocodilian body from its tail in the literature for several centuries, it has been assumed during those hundreds of years that everyone knew the details of the technique, and therefore it has not been defined in precise terms. There are possibly two different options, because the proximal end of the back edge of the hind limb is often slightly anterior to the level of the back edge of the major femur-bone zone muscle-mass and thicker skin just a little way further away from the base of the tail (more distal from the long-axis of the animal). In other words, the hind-limbs have a variable circumpherance or diameter, depending on at what level it is measured. The back leg is thin at its attachment, compared with being thicker just a short distance away from the body.

The method employed by the Zoer 2006-2007 expedition was the muscle-mass level, with the hind-limbs outstretched, as illustrated in Figure 5.3, because the few published (and crude) diagrams in the literature seem to suggest it. Although only a guess, this decision was an attempt in good-faith to replicate the experiments of colleagues, but this time with the Ross + Mayer (1983) method’s results as a control.

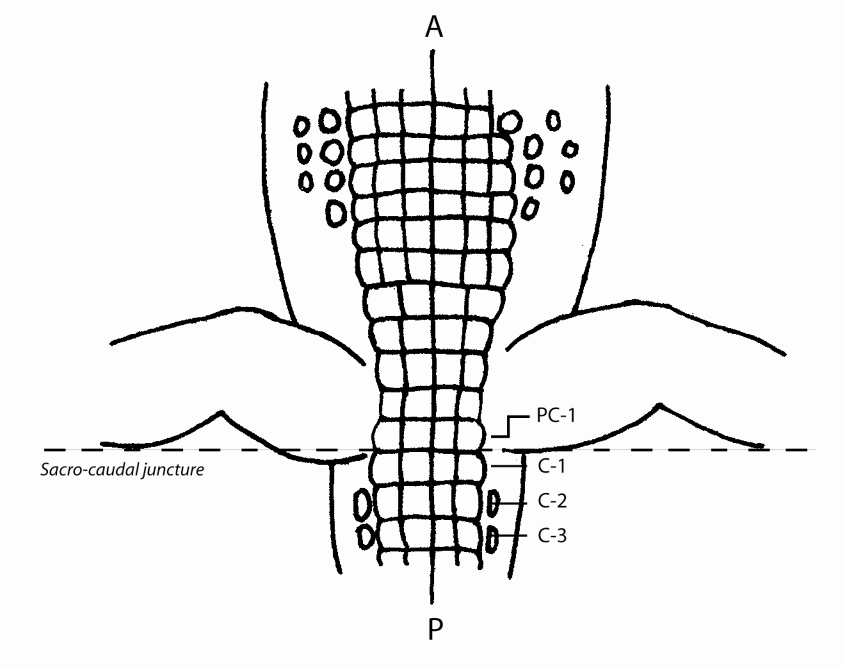


Figure 5.3 Transverse level of posterior edge of the back legs
The outstretched hind-limbs of a male specimen (XXL-108), *Osteolaemus tetraspis* Cope, from Congo-Brazzaville at Bellelo. This Atlantic coast animal is 28 cm in length and the imaginary line across the posterior edge of muscle-mass indicates the division between body and tail.

If the assertion that the posterior edge of the back-legs reliably locates the sacro-caudal juncture in all of the African dwarf-crocodiles sampled in 2006-2007 by the Zoer *Osteolaemus* fieldwork project is true, then it has a good probability of applying to specimens outside the study zone also, because photographs of dwarf-crocodiles from the Gambia River in Senegal (Villiers 1958:322, figure 288), and also from the Ituri Forest in northeastern Zaïre-DRC (Schmidt 1919) appear to have the same short and thick hind-limbs that were encountered while collecting the data reported in Table 5.3, which includes both wild and captive *Osteolaemus tetraspis* Cope.

Table 5.3 Back edge of the hind-legs works? True.

Methods of finding PC-1 and the SC-J	success rate
Manually feeling the iliac crest (old constant)	68 out of 68
Manually stretching the femurs (old constant)	49 out of 49
Relative trans. width of row PC-1 (new constant)	67 out of 68
Back edge of hind legs (the new tested variable)	68 out of 68

All four methods employed to find PC-1 and to determine the sacro-caudal juncture (SC-J), in the Zoer 2006-2007 *Osteolaemus tetraspis* Cope sample from five equatorial western African nations, worked.

The 100% (in one case almost 100%) positive result in Table 5.3 implies that this character does not change as the African dwarf-crocodile grows from being a very small hatchling to a bulky and sometimes really big adult. The range of variation in total length of the individual *Osteolaemus* reported in Table 5.3 was 20,5 cm to 163,15 cm, measured snout-tip to tail-tip above the animal, and also below the animal, and the two lengths were averaged together, as already detailed in Chapter 1 (above).

5.3.3 Anteriormost post-cloacal caudal whorl locates the sacro-caudal juncture, true or false?

Earlier (in Section 5.3.1) it was noted that the difference between dorsal-armour characters and ventral-scalation characters is highly significant on the crocodilian throat, collar, thorax, abdomen or pelvic, and cloacal regions (the belly-skin exclusive of its post-cloacal tail), because there is absolutely no direct correlation between the dorsal (tied to the vertebral column) and precaudal ventral (free floating and unanchored) scalations. Although the cloacal obstruction zone is often called the cloacal “oval” in the literature, that term is an oversimplification, but well worth mentioning, because the flexible skin where the female crocodile expels her eggs from her body (the cloaca is the exit for liquid and solid waste, and also the crocodilian genital and reproductive opening) is usually some variation on an ovalish shape.

Behind the cloacal obstruction, the ventral transverse rows of scales on the under surface of the tail are continuations of transverse rows of dorsal armour. The upper and lower scales are connected on the lateral surfaces of the tail by a contiguous series of subdorsal scales. The combination of the dorsal, lateral, and also the ventral scales makes a continuous ring around the crocodilian tail, called a caudal "whorl" of scales, similar to whorls of leaves or flowers arranged around and encircling the stem of a plant.

The first and most anterior caudal whorl to pass posterior to the cloaca is the first transverse row of scales that, even if narrowed to some degree, does not get broken (separated into two pieces) along the ventral long-axis midline of the base of the tail. There is the possibility that caudal whorls other than C-3 will be the scale row in question (Figures. 5.5 and 5.6), but arbitrarily following Ross + Mayer (1983:fig. 11-B), the third caudal row (C-3) was adopted as the tested norm in this thesis, as illustrated in Figure 5.4 (below). Thus, in the analysis that follows, C-2 and C-4 are considered to be variation from the theoretically expected C-3 outcome.

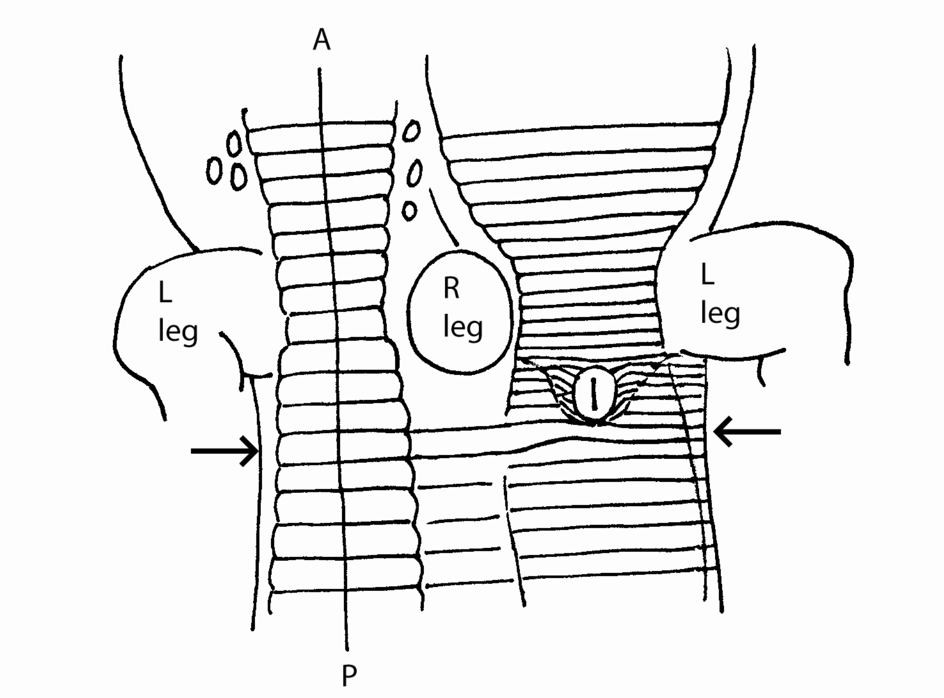


Figure 5.4 C-3 can be the anteriormost caudal row to pass posterior to the cloaca on the ventral surface of the tail

The third (3rd) caudal row on this male specimen is the anteriormost caudal row to pass posterior to the cloacal oval on the ventral surface of the tail. The origin of this *Osteolaemus tetraspis* Cope (XXL-124) is Congo-Brazzaville COAST at Youbi.

In addition to the third caudal row (C-3, illustrated in Figure 5.4) being the answer to this question, the second caudal whorl (C-2) also occurred, as shown below in Figure 5.5, and thus there is some variation in this character in *Osteolaemus tetraspis* Cope.

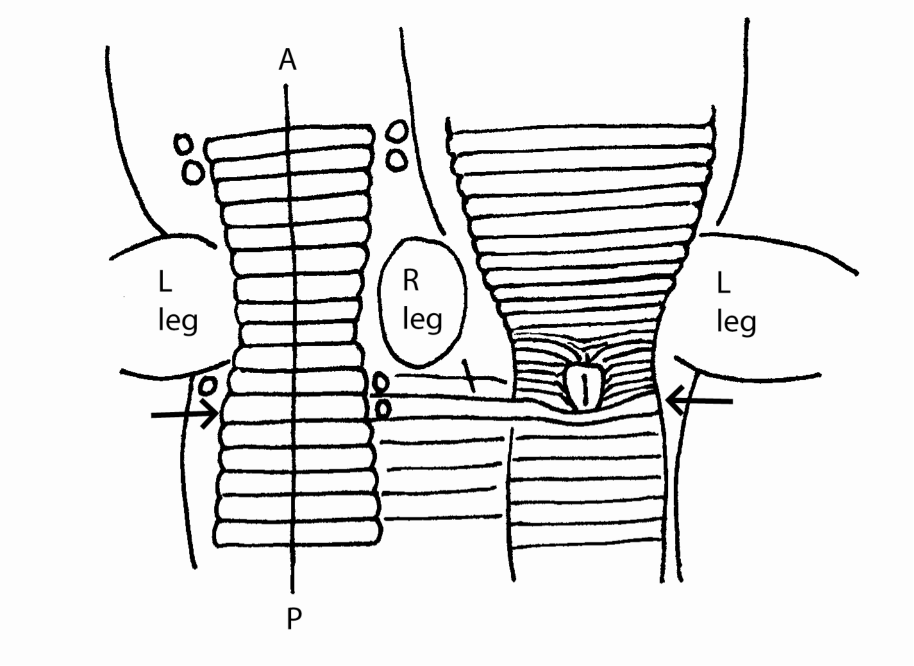


Figure 5.5 C-2 can be the anteriormost caudal row to pass posterior to the cloaca on the ventral surface of the tail

The second (2nd) caudal row on this male specimen (XXL-109) Congo-Brazzaville COAST at Bellelo is the anteriormost caudal row to pass posterior to the cloacal oval on the ventral surface of the tail. This *Osteolaemus tetraspis* Cope from Congo-Brazzaville COAST is 28,8 cm in length.

In addition to the third and the second caudal rows being the answer to this question, the fourth caudal whorl (C-4) also occurred. This third and last character option encountered in the Zoer 2006-2007 *Osteolaemus tetraspis* Cope field-sample is presented in Figure 5.6, below.

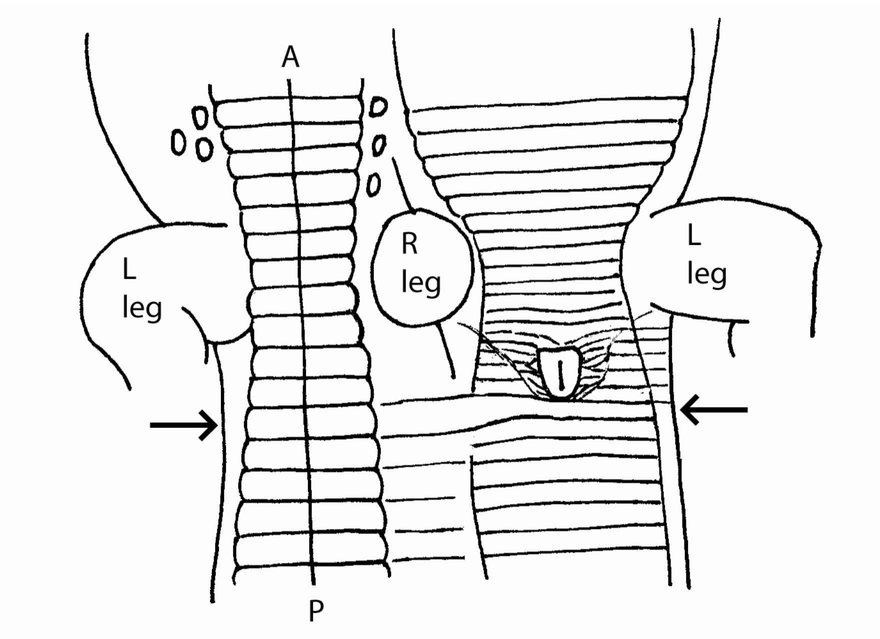


Figure 5.6 C-4 can be the anteriormost caudal row to pass posterior to the cloaca on the ventral surface of the tail

In this male specimen (XXL-17) Congo-Brazzaville INTERIOR at Kinshasa the fourth (4th) caudal row is the anteriormost caudal row to pass posterior to the cloacal oval on the ventral surface of the tail. This African dwarf-crocodile from Congo-Brazzaville INTERIOR, *Osteolaemus tetraspis osborni* (K.P. Schmidt), is 143,6 cm in length.

Thus, there are three available options about which dorsal caudal row (C2, C-3, or C-4) corresponds with the first row on the ventral surface of the tail posterior to the cloaca. The occurrence rates of these three outcomes in this 2006-2007 sample are compared in Table 5.4 below, and will be analysed for possible correlation with geography or sex.

Table 5.4 Three individual transverse rows can be the first post-cloacal

First caudal whorl to pass behind the vent	occurrences
Second caudal row (C-2) = probable variable	4 out of 42
Third caudal row (C-3) = possible constant	36 out of 42
Fourth caudal row (C-4) = probable variable	2 out of 42

The third (3rd) caudal row is not a constant, because only 36 out of 42 (= 85,7%) animals have C-3 as the first post-cloacal transverse row. In addition, two other differing options (C-2 and C-4) definitely occur, though both of these variations are relatively infrequent.

Although the third caudal row occurs in a high frequency as the first post-cloacal whorl, the result in Table 5.4 above is still not a 100%. Therefore further analysis for geographic variation and sexual variation is desirable. The locality variable is here reviewed first in Table 5.5 below. The results from African dwarf-crocodiles representing five geographic localities in this sample are analysed in an attempt to find subspecies.

Table 5.5 Geographic distribution of post-cloacal whorl results among specimens in the Zoer 2006-2007 sample (n=42)

Three possibilities for the 1st post-cloacal	localities
Osteolaemus with C-2 the answer (n=4)	A = 1 of 6; D = 3 of 27
Osteolaemus with C-3 the answer (n=36)	A = 5 of 6; C = 8 of 8; D = 23 of 27
Osteolaemus with C-4 the answer (n=2)	B = 1 of 1; D = 1 of 27

Table 5.5 contains data for African dwarf-crocodile specimens from the following four localities: A = Congo-Brazzaville COAST; B = Zaïre-DRC INTERIOR (at Kinshasa); C = Gabon COAST; D = Cameroon COAST. An answer of C-4 can rarely occur in *O. t. tetraspis* and also in *O. t. osborni*. It is probable that an answer of C-3 occurs frequently in *O. t. osborni* when a larger sample is available.

There does not seem to be an affirmative correlation between the locality of the specimen and any of the three possibilities of dorsal caudal whorls corresponding with the first post-cloacal row on the belly side of the crocodile. Note that unfortunately only one African dwarf-crocodile from the inland of Africa is present in this table (Zaïre-DRC INTERIOR, at Kinshasa). The other INTERIOR locality in the 2006-2007 sample, Congo-Brazzaville (along the Ubangi River), is completely absent from this table, because circumstances in the field did not always allow the researchers to collect all possible data on crocodiles encountered during the expedition.

The sex of a specimen could be another possible explanation for one of the three possibilities (C-2, C-3 or C-4) being the dorsal caudal row corresponding with the ventral first post-cloacal row, as shown in Table 5.6.

Table 5.6 Sex data for *Osteolaemus* with C-2, C-3 or C-4 being the corresponding row

Three possibilities for the 1st post-cloacal	how many of each sex
Osteolaemus with C-2 the answer	3 males, 1 female, 0 no data
Osteolaemus with C-3 the answer	12 males, 10 females, 14 no data
Osteolaemus with C-4 the answer	0 males, 1 female, 1 no data

Table 5.6 shows sex data for African dwarf-crocodile specimens from four localities (see caption Table 5.5) sampled in 2006-2007 by the Zoer *Osteolaemus* project. Sex was not recorded on 15 out of the 42 possible African dwarf-crocodiles, for various practical reasons, none of which make these results invalid, except that in total the individuals that are missing data has significantly decreased the size of the sample.

From the limited data in Table 5.6 about sex, it is clear that an animal with C-2, C-3 or C-4 could be a female. Similarly, Table 5.5 earlier had C-4 in both the COAST and the INTERIOR categories, with a high probability of overlap in C-3 answers occurring in a larger sample of INTERIOR *O. t. osborni* animals.

Thus, in contrast with the high reliability of the back-legs method agreeing with the results of the Ross + Mayer (1983) criteria for locating the sacro-caudal juncture between PC-1 and C-1, it appears that correlations between caudal vertebrae (the dorsal armour) and the first post-cloacal ventral whorl variations are unfortunately reliable predictors of neither geography (with regard to COAST and INTERIOR localities) nor the sex of the animal.

The most significant result in this chapter is that all of the four different methods of finding the first pre-caudal transverse dorsal row, at the pelvis and back legs region, agree with each other. This finding is of no direct taxonomic importance, but it does allow the new data about the dorsal armour on the *Osteolaemus* tail to be compared with the published data about double-crested caudals (DCC's) in the literature, where the variation in numbers of DCC's has been considered taxonomically important by some authors, as detailed below in Table 5.7, and will be discussed at length in Chapter 6 (below).

Table 5.7 Sources of published DCC numbers, arranged chronologically

Year	author	DCC's	taxon
1919	Schmidt	12 - 14	*O. t. osborni*
1948	Inger	11	*O. t. tetraspis*
1948	Inger	12 - 14	*O. t. osborni*
1973	Brazaitis	10 - 12	*O. t. tetraspis*
1973	Brazaitis	12 - 14	*O. t. osborni*
1983	Wermuth + Fuchs	11 - 13	*Osteolaemus tetraspis*
1983	Ross + Mayer	10 - 14	*Osteolaemus tetraspis*
1995	Charette	10 - 12	*O. t. tetraspis*
1995	Charette	12 - 14	*O. t. osborni*
2006	Fuchs	10 - 12	*O. t. tetraspis*
2006	Fuchs	12 - 14	*O. t. osborni*

The double-crested caudals (DCC's) range of 12-14 in the INTERIOR subspecies has remained unchanged from 1919, through 1948 and 1973 and 1995 to 2006. In contrast, the COAST subspecies started at 11 DCC's in 1948, and then increased to 10-12 DCC's in 1973, and has stayed at 10-12 through 1995 and 2006.

The Inger (1948) data in Table 5.7 was the first comparative listing of double-crested caudal numbers for the *Osteolaemus t. tetraspis* and *O. t. osborni* subspecies, and it was the only report of comparative DCC numbers that did not include 12 DCC's in both taxa. The Zoer 2006-2007 *Osteolaemus tetraspis* sample is considerably larger than most or all other reports on this subject, and thus it is possible that the range of variation in the number of DCC's will be found to be of taxonomic utility in Chapter 6, but the recent literature has already suggested that complete separation between the two subspecies is not expected to be accomplished with the C.I.T.E.S. character. Thus, Chapter 6 will ask two questions. Could differences in counting techniques at the posterior end of the DCC's cause different observers to count DCC's differently? Does larger sample size increase or decrease the range of overlap in DCC's between *O. t. tetraspis* and *O. t. osborni* as they are geographically defined by C.I.T.E.S.?

5.4 REVIEWING THE SACRO-CAUDAL JUNCTURE INCLUDING THE HIND-LEGS METHOD

Although the back legs on *Osteolaemus* have thighs of great girth, and therefore exhibit a curved posterior surface, the old literature method of locating the start of the tail, at the back edge of the thighs, works reliably well and thus the leg-edge results can be correlated reliably with the three other methods (the pelvis, the femurs, and the monotonic width). This is good news, but Chapter 5 had no direct bearing on the taxonomic question of subspecies in *Osteolaemus tetraspis* other than finding in Chapter 5 that the anteriormost post-cloacal ventral caudal whorl is a variable that does not appear to be predictive for separating *O. t. tetraspis* from *O. t. osborni*; when the COAST and INTERIOR geographic and ecological categories are defined by C.I.T.E.S. as whole nations (except Congo-Brazzaville, which has both categories).

CHAPTER VI TESTING THE INGER (1948) DOUBLE-CRESTED CAUDAL SCALES HYPOTHESIS

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

6.1 INTRODUCTION

The transverse level where division occurs between the body and the tail generated not only the first precaudal row on the body, but also the first caudal row to be present on the tail. The number of continuous precaudal rows on the body of *Osteolaemus tetraspis* Cope, the African dwarf-crocodile, will be discussed in Chapter 7-9 (below), but here in Chapter 6 only the tail (caudal series) is addressed. Posterior to PC-1, the caudal series consists first of proximal double-crested caudals (DCC's) and then distally of single-crest caudals (SCC's). Figure 6.1 shows an African dwarf-crocodile with the two kinds of caudals indicated on its tail.

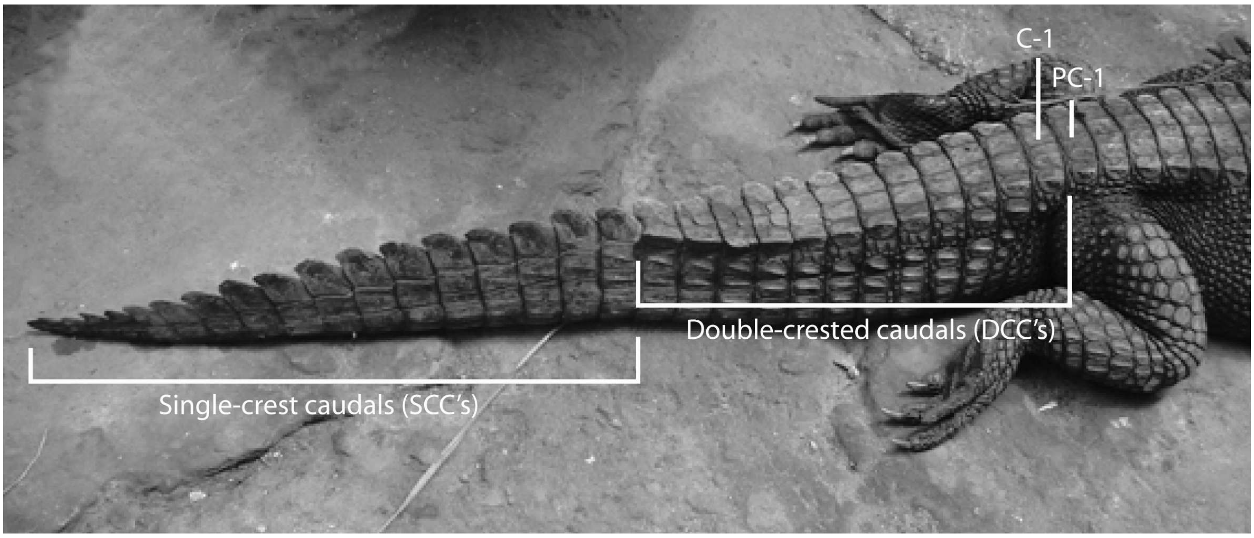


Figure 6.1 Tail with series of double-crested and single-crest caudals

This female dwarf-crocodile (XXL-123) from Congo-Brazzaville at Likouala River has the series of DCC's and the series of SCC's on the tail indicated by ventral and lateral brackets. The transverse level where division occurs between the body and the tail is indicated dorsally with PC-1 and C-1.

Because the sacro-caudal juncture (SC-J) can be reliably located by four different methods in the African dwarf-crocodile (two manual skeletal ways, and two visual ways) as established above in Chapter 5, the anterior end of the double-crested caudal series of dorsal transverse scale-rows is available on whole animals, on flat and stuffed skins, and from photographs. The first caudal row (C-1) is the transverse row immediately posterior to the first precaudal row (PC-1). The double-crested caudals (DCC's) start at the sacro-caudal juncture (SC-J) with C-1 and then proceed through C-2 and C-3 and continue to a variable level (anywhere between C-9 and C-21 are possible amongst the living crocodilian species as a group), where the double-crested caudals series ends, and posterior to it the single-crested caudals series begins.

The genera *Paleosuchus* and *Caiman* in the alligator subfamily, and the genus *Osteolaemus* in the crocodile subfamily, share the characteristic of having very few transverse rows of double-crested caudals (DCC's), while the gharial of the Ganges (*Gavialis*) and the Indo-Pacific saltie (*Crocodylus porosus*) share the characteristic of having very many DCC's (Ross + Mayer 1983:328). Among the three African species of crocodilians, *Crocodylus cataphractus* has 16 or 17 DCC's (n=12), while *Croc. niloticus* ordinarily has 16 to 19 (and one with 21 when n=25), so all of the slender-snouted *C. cataphractus* are within the range of variation of the Nile crocodile species. However, the Ross + Mayer (1983:328) table gives *Osteolaemus tetraspis* a range of 10 to 14 DCC's (n=18, with 12 the most frequent), which distinguishes the dwarf-crocodile from its continental companions.

The most proximal of the double-crested caudal rows is C-1, and in the genus *Osteolaemus* Cope it is four scales in a transverse and contiguous series crossing the dorsal surface of the base of the tail. None of the four dorsal scales in C-1 has any remarkable keel on it, nor do any dorsal scales in C-2 or C-3 have high keels. However, somewhere around the sixth caudal row (C-6) the four dorsal scales in each row start to become reduced to three-across, and on the lateral edges of the dorsal surface of the dwarf-crocodile's tail, the lengthwise (long-axis of the tail) keel rows that give the double-crested caudals (DCC's) their name, begin to develop.

Numerous authors (Brazaitis, 1973:79-80; Wermuth + Fuchs, 1983:vol. 3; Charette, 1995:9 orange; and Fuchs, 2006:132-137) have claimed that there is overlap between the ranges of variation in DCC's between the two subspecies. The overlap is narrowed to row C-12 by some authors (Brazaitis, 1973:79-80; Charette, 1995:9 orange; and Fuchs, 2006:132-137). The exception to the general rule is Inger (1948:18) who found no overlap in the DCC character, as already shown in Table 5.7, above.

In Section 6.2 the actual counting of the qualifying transverse caudal rows on the tail is discussed. In Section 6.3 the results of the character "double-crested caudals" are later presented and analysed country by country.

6.2 METHODS

The anterior starting point for counting the number of double-crested caudals is located at the anterior end of the tail. However, in this chapter only the transverse caudal rows anterior to the point at which the tail crest becomes single are considered. The posterior point of division between the double-crested caudals series and the single-crest caudals series has to be clearly defined. The anterior and posterior ends of the double-crested caudal series can been seen in Figure 6.2, below.

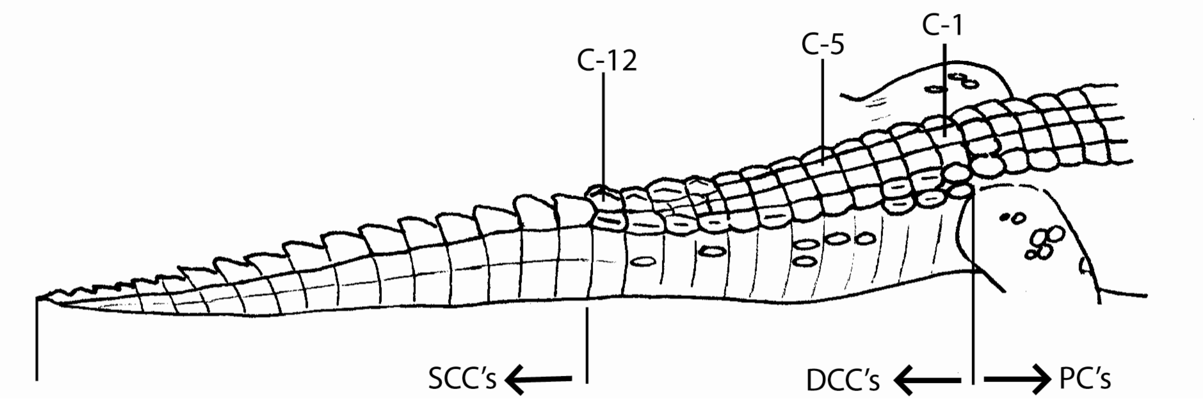


Figure 6.2 Counting DCC's on the tail

This female African dwarf-crocodile from Congo-Brazzaville at Likouala (= INTERIOR) shows the number of double-crested caudals on its tail. When counting away from the sacro-caudal juncture (= posteriorly; towards the tip of the tail) 12 DCC's are distinguishable on this specimen.

From the literature it is known that in *Osteolaemus tetraspis* Cope the symmetrically disposed pair of enlarged keels normally become really noticeable by about C-10 and C-11, and by C-12 the entire strictly dorsal transverse row normally consists of only the two scales that have big keels (Ross + Mayer (1983:328). When there are 12 DCC's, it means that C-12 is a double-crested caudal (DCC) as opposed to a single-crested caudal (SCC) transverse row. In this case C-13 is the most anterior of the latter group. The DCC rows correspond in the one-to-one relationship with vertebrae of the tail that have transverse processes (see Ross + Mayer's figure 2), while the SCC rows correspond with caudal vertebrae that lack transverse processes. The transition from vertebral centra with transverse-processes to those without processes is very gradual and the division line between the two skeletal character states is generally indistinct, as can also the external (DCC's, SCC's) division be indistinct on some crocodilians.

The same way that the transition from one kind of caudal vertebra to another was indistinct (above), sometimes within the living Crocodylia the transition from double-crested caudals (DCC's) to single-crest caudals (SCC's) is less than clear. In some species it is possible to encounter one row that demands close inspection and some thought, because one dorsal keel rises from the tail, yet it bifurcates into two crests at its apex. Because the name of the character is double-crested caudals, those two tiny little crests count. In some animals in some species a cross-section Y-shape occurs in the area of the tail where the crest becomes single. In these cases, the Y-shaped caudal would be added to the number of double-crested caudals in this study. Figure 6.3 shows the range of theoretical variation, with the arrow indicating the anteriormost scale of the single-crested caudals series.

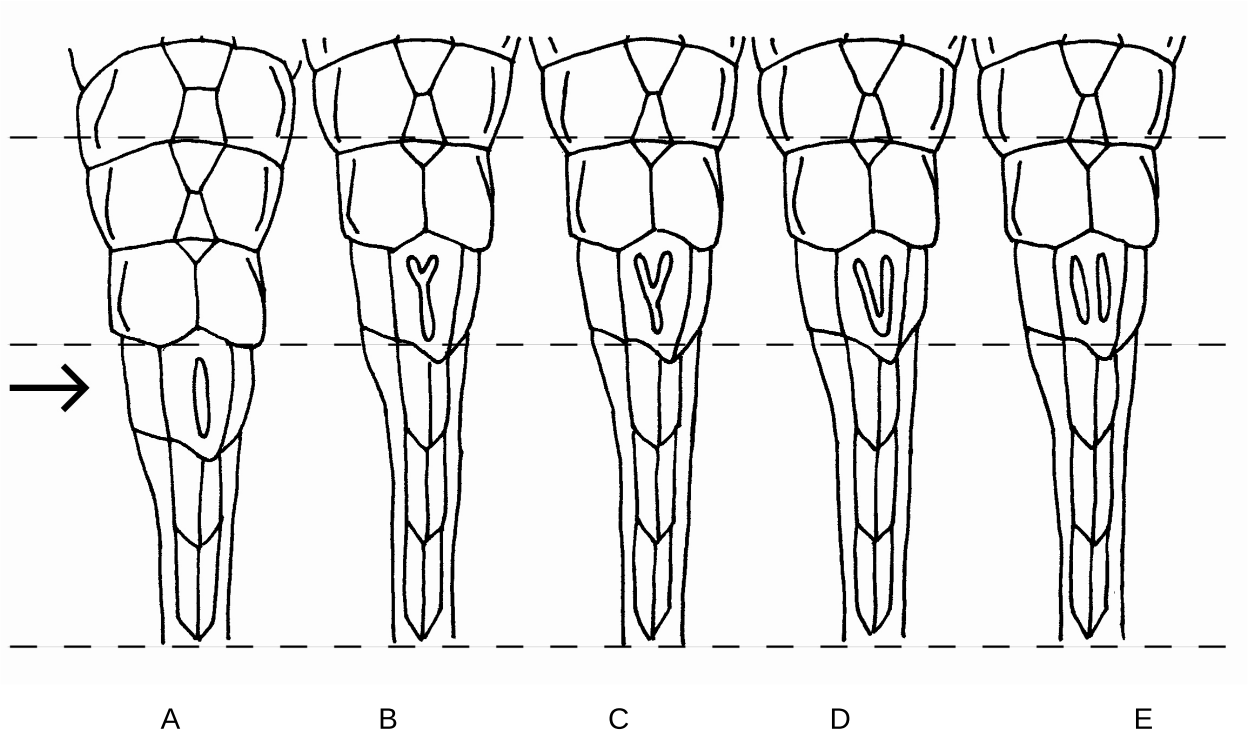


Figure 6.3 Sometimes the distinction between double-crested caudals (DCC's) and single-crest caudals (SCC's) is less than clear (in theory), but it is apparently clear in the genus *Osteolaemus*
This diagrammatic series shows five distinct options. Of the five, only option A occurred in the Zoer 2006-2007 sample. (A) this male dwarf-crocodile (XXL-124) from Youbi (Congo-Brazzaville) shows a clear distinction between its double-crested caudal series, and its single-crest caudals. In contrast, diagrams B + C show variations of a Y-shaped caudal scale, and diagram D shows a V-shaped caudal scale. The double crested-caudal (E) can also be attached at the base of the keels, while separated at the crests.

The number of double-crested caudals on each tail was systematically recorded on a field protocol. In special cases, or as a general sample selected at random, pictures were taken for future comparison with the data collected in this study, and with other studies. For the same reason, some detailed drawings of this character were made in the field.

6.3 RESULTS

The results about the number of double-crested caudals on the tail in *Osteolaemus* will be displayed in two subsections. In Subsection 6.3.1 the number DCC's in *Osteolaemus* is presented and analysed country by country. To compare the results of specimens from the Atlantic Ocean coastal nations with the animals from the interior of the continent, the number of DCC's is also displayed by region, and Subsection 6.3.1 deals with this COAST and INTERIOR comparison.

As mentioned in the methods section (above), sometimes the distinction between double-crested caudals (DCC's) and single-crest caudals (SCC's) is less than clear in some species. However, as shown in Table 6.1 below, all of the *Osteolaemus* encountered by the 2006-2007 expedition had fairly clear and unambiguous distinctions from the two keeled state (DCC's), to the one keeled state (SCC's), without any complications.

Table 6.1 Double-crested caudals have their posterior limit obvious to anyone

Limit of DCC's where the SCC's start	frequency
Distal DCC is clearly two keels, no problem	68 out of 68
Distal DCC is ambiguous but not single crest	0 out of 68

The clarity of the posterior limit of double-crested caudals of African dwarf-crocodiles is displayed in this table. Without exception every *Osteolaemus* encountered by the Zoer 2006-2007 expedition had a fairly clear and unambiguous distinction.

The most frequent range of variation in the number of double-crested caudals (DCC's) is 11 to 14, though Ross + Mayer (1983:328) reported one with only 10 DCC's. The famous Robert Inger (1948: Copeia magazine) paper gave the range as 11 to 14, which was taxonomically divided into *Osteolaemus tetraspis* Cope (always with 11 DCC's in a small sample), compared with *Osteolaemus osborni* (Schmidt) which never has 11 DCC's in a small sample, and thus always has 12 or 13 or 14 double-crested transverse dorsal caudal rows. The Inger hypothesis (modernized) is thus that the two subspecies of *Osteolaemus* Cope can be identified to subspecies by a scale-count character.

The Zoer 2006-2007 expedition sample of 68 African dwarf-crocodiles includes material from both sides of the subspecies boundary between *Osteolaemus tetraspis tetraspis* Cope along the Atlantic Ocean coast, compared with *Osteolaemus tetraspis osborni* (Schmidt) from the interior of the continent, specifically at Kinshasa in Zaïre-DRC, and from a tributary of the Ubangi River in the northern and eastern interior of Congo-Brazzaville. Thus it is possible to test Robert Inger's (1948:18) assertion here, in Table 6.2 presented as animals identified to C.I.T.E.S. subspecies.

Table 6.2 Testing the Inger hypothesis with bigger samples (53 COAST, and 15 INTERIOR)

Osteolaemus subspecies name	numbers of DCC's	frequency
O. tetraspis tetraspis Cope	distal end is C-11	15 out of 53
O. tetraspis osborni (Schmidt)	distal end is C-11	0 out of 15
--- --- --- --- ---		
O. tetraspis tetraspis Cope	distal end is C-12	29 out of 53
O. tetraspis osborni (Schmidt)	distal end is C-12	2 out of 15
--- --- --- --- ---		
O. tetraspis tetraspis Cope	distal end is C-13	8 out of 53
O. tetraspis osborni (Schmidt)	distal end is C-13	11 out of 15
--- --- --- --- ---		
O. tetraspis tetraspis Cope	distal end is C-14	1 out of 53
O. tetraspis osborni (Schmidt)	distal end is C-14	2 out of 15

None of the 15 individual *Osteolaemus tetraspis osborni* (Schmidt) subspecies specimens examined during the Zoer 2006-2007 expedition had eleven double-crested caudals on its tail. Although this result partly confirms the Inger hypothesis, there is variation in the number of DCC's in the larger sample from coastal areas (*Osteolaemus tetraspis tetraspis* Cope). The number of DCC's in this latter (n=53) subspecies varies between eleven (11) and fourteen (14).

Although all C.I.T.E.S. subspecies were consciously avoided by Ross + Mayer (1983), the Museum of Comparative Zoology study included African dwarf-crocodile specimens from both geographic sides of the subspecies boundary, and thus the total variation should in theory include having C-10 as the most distal transverse row of double-crested caudals (DCC's). This latter range of variation (10-11-12-13-14) in *Osteolaemus* is five choices (of which C-10 did not occur in either the Inger sample or in the Zoer sample).

Before examining the 2006-2007 expedition's results on a nation by nation basis, and before looking for possible correlations with sex, note that a range of variation of about five transverse rows in the DCC's is fairly common among the living crocodilians, and variation of four and three rows is very frequently encountered even within a single species.

The identification of African dwarf-crocodile subspecies by means of the number of double-crested caudal (DCC) transverse scale-rows is not a simple question, and Section 6.3.1 is required for completeness about this Inger (1948), and C.I.T.E.S. (1974 to the present) character, which is considered by some to be of taxonomic utility in the *Osteolaemus* subspecies dichotomy.

6.3.1 Further testing of Inger's and other hypotheses

In the Zoer 2006-2007 expedition's *Osteolaemus* data there are two samples that are very small. One is Benin on the Atlantic Ocean coast (n=1), and the other is Kinshasa in the interior (n=1). Because the Benin animal is clearly *Osteolaemus tetraspis tetraspis* Cope, by geography, Table 6.3 tests Dr. Inger's assertion that 11 is the only answer.

Table 6.3 DCC extent on one animal from COAST at Benin

Osteolaemus subspecies	distal end of DCC series is
O. tetraspis tetraspis Cope	the 12th caudal row (C-12)

This animal (XXL-185; sex unknown) from the vicinity of Porto Novo in Benin (examined as a long-term captive) has the condition that Ross + Mayer (1983:328) predicted as the most common in the African dwarf-crocodile species (9 out of n=18 in the Harvard report). Obviously Inger's sample was too small. This animal (XXL-185) would be incorrectly identified at the subspecies level, because Inger's (1948) prediction from geography was that a Benin *Osteolaemus* would have 11 DCC's.

The other national sample of only one individual in the Zoer 2006-2007 expedition results is Kinshasa in Zaïre-DRC, which is taken to mean "Stanley Pool" in the type description (Table 6.4, below), and is thus within the geographic distribution and range of the taxon *Osteoblepharon osborni* Schmidt.

Table 6.4 DCC extent on one animal from INTERIOR at Zaïre-DRC

Osteolaemus subspecies	distal end of DCC series is
O. tetraspis osborni (Schmidt)	the 13th caudal row (C-13)

This female (XXL-17) from near the city of Kinshasa has an acceptable number of double-crested caudals (DCC's) for its subspecies according to Inger (1948), but the size of the sample (n=1) is remarkably small. However, the characteristic of having thirteen DCC's does definitely occur at the type locality of *Osteoblepharon osborni* Schmidt, and this individual agrees with the literature sample from northeastern Zaïre-DRC reported by Schmidt (1919) and Inger (1948).

The city of Kinshasa in Zaïre-DRC is located at the southwestern corner of the theoretical geographic distribution of *Osteoblepharon osborni* Schmidt, according to the understanding of Herbert Lang, the American Museum of Natural History (AMNH) expedition member who collected the type series in the Ituri Forest region, and Mr. Lang was sure in his own mind that African dwarf-crocodile habitat of the “inland” and “interior” kind (far away from the Atlantic coast, above and including “Stanley Pool” = near Kinshasa today, and typified by the Ubangi River drainage) is continuous from the Ituri Forest to Kinshasa. Also Mr. Lang (in Schmidt, 1919) also explicitly asserted that the limit of today's *Osteolaemus tetraspis osborni* (Schmidt) distribution is Kinshasa (any closer to the coast while going down the Congo River is *Osteolaemus tetraspis tetraspis* Cope).

The Zoer 2006-2007 African dwarf-crocodile sample included fourteen *Osteolaemus* from north of “Stanley Pool” (the donut shaped widening in the Congo River just north of Kinshasa). This n=14 collection is significantly close to the type locality of *Osteoblepharon osborni* Schmidt, because the Likouala River is a tributary of the Ubangi River, north of the confluence of the Ubangi with the Congo. Although politically located in Congo-Brazzaville, the sample in Table 6.5 (below) is representative of Ubangi River drainage in Zaïre-DRC nation on the other side of the river, because the Ubangi is an international border. All of the entire Ubangi River drainage is geographically inside Schmidt’s and Lang’s INTERIOR taxon as it is understood today.

Table 6.5 DCC extent on animals from the Likouala INTERIOR part of Congo-Brazzaville, plus individual sex data when known

XXL #	*Osteolaemus* subspecies	back end of DCC's	sex
#110	*O. tetraspis osborni* (Schmidt)	is C-13	male
#111	*O. tetraspis osborni* (Schmidt)	is C-14	male
#112	*O. tetraspis osborni* (Schmidt)	is C-13	female
#113	*O. tetraspis osborni* (Schmidt)	is C-12	no data
#114	*O. tetraspis osborni* (Schmidt)	is C-13	no data
#115	*O. tetraspis osborni* (Schmidt)	is C-13	no data
#116	*O. tetraspis osborni* (Schmidt)	is C-13	no data
#117	*O. tetraspis osborni* (Schmidt)	is C-13	no data
#118	*O. tetraspis osborni* (Schmidt)	is C-13	male
#119	*O. tetraspis osborni* (Schmidt)	is C-13	male
#120	*O. tetraspis osborni* (Schmidt)	is C-13	male
#121	*O. tetraspis osborni* (Schmidt)	is C-13	male
#122	*O. tetraspis osborni* (Schmidt)	is C-14	female
#123	*O. tetraspis osborni* (Schmidt)	is C-12	female

As far as sex is concerned, the two animals (#111 and #122) with fourteen DCC's cancel each other out, being one male and one female. Two animals (#113 and #123) are the lowest counts with twelve DCC's, being one female and one without sex data. However, the majority of the Likouala River specimens (10 out of 14) have thirteen DCC's, being five males, one female and four with no data. The sex ratio (when known = random) appears random about which sex has twelve (12), thirteen (13) or fourteen (14) DCC's. The significant result is that C-11 does not occur in this sample of 14 Likouala animals from the INTERIOR, agreeing with the one specimen (above) from Kinshasa which was also not C-11.

The comparison (begun with Benin) among COAST animals continues now with specimens from Congo-Brazzaville at Pointe-Noire, Bellelo, Youbi and Dembouanou in Table 6.6, below.

Table 6.6 DCC extent on animals from the COAST part of Congo-Brazzaville, plus sex data

XXL #	locality in coastal zone	subspecies	back end of DCC's	sex
#104	Pointe-Noire	*O. t. tetraspis*	is C-12	no data
#105	Pointe-Noire	*O. t. tetraspis*	is C-12	no data
#106	Bellelo	*O. t. tetraspis*	is C-12	female
#107	Bellelo	*O. t. tetraspis*	is C-12	female
#108	Bellelo	*O. t. tetraspis*	is C-12	male
#109	Bellelo	*O. t. tetraspis*	is C-12	male
#124	Youbi	*O. t. tetraspis*	is C-11	male
#125	Dembouanou	*O. t. tetraspis*	is C-12	male
#126	Pointe-Noire	*O. t. tetraspis*	is C-11	no data
#127	Pointe-Noire	*O. t. tetraspis*	is C-12	no data
#128	Pointe-Noire	*O. t. tetraspis*	is C-11	male

Three African dwarf-crocodiles (XXL-124, #126, and XXL-128) have eleven DCC's, being two males and one with no data. The other specimens from the sample (n=11) all have twelve DCC's. Five of them are with sex (3 males, 2 females). Nation of "Congo" is called Congo-Brazzaville to keep it separate from the other "Congo" nation called Zaïre-DRC for clarity in this thesis. The significant development here is that C-11 is not the only outcome.

Because the Atlantic Ocean coastal ecology is continuous across the political border between Congo-Brazzaville (the COAST part) and its neighbour to the north, the nation of Gabon (COAST), it is predicted that the variation in the number of double-crested caudal (DCC) rows in Gabon (see Table 6.7 below) will be similar to that in Tab. 6.6 for the COAST part of Congo-Brazzaville (above).

Table 6.7 DCC extent on animals from COAST at Gabon, plus sex when known

XXL #	locality	*Osteolaemus* subspecies	back end of DCC's	sex
#130	Kango	*O. tetraspis tetraspis*	is C-12	female
#132	Kango	*O. tetraspis tetraspis*	is C-11	male
#134	Setté Cama	*O. tetraspis tetraspis*	is C-11	female
#135	Setté Cama	*O. tetraspis tetraspis*	is C-12	female
#136	Setté Cama	*O. tetraspis tetraspis*	is C-12	male
#137	Setté Cama	*O. tetraspis tetraspis*	is C-12	male
#138	Setté Cama	*O. tetraspis tetraspis*	is C-12	female
#139	Gamba	*O. tetraspis tetraspis*	is C-12	no data

In this Gabon sample (n=8), C-11 and C-12 are the alternatives for the distal end of the double-crested caudal series. The single male (#132) and female (#134) with eleven DCC’s cancel each other out. The sex ratio in specimens with twelve DCC’s is almost in balance (2 males, 3 females and one with no data).

As predicted, the Gabon sample (n=8) resembles the coastal sample from Congo-Brazzaville (n=11). The total observed variation in the coastal sample at this point (n=19) in the analysis is that C-11 and C-12 (but no others) can be the distal end of the double-crested caudal (DCC) series. In other words, no C-10 has been found, and significantly, absolutely no C-13 or C-14 have occurred in the *Osteolaemus tetraspis tetraspis* Cope sample when n=20 (Congo-Brazzaville coast, Gabon and Benin). Fortunately, the Zoer expedition’s 2006-2007 sample from tropical Africa includes the nation of Cameroon (n=33), situated between Gabon and Benin, and entirely coastal. Thus the Cameroon sample in Table 6.8 will test the hypothesis that twenty specimens (n=20) is sufficient for characterizing the range of variation in DCC’s in an *Osteolaemus* Cope subspecies.

Table 6.8 Animals from Cameroon are COAST, in four sub-tables (A-D)

Sub-table 6.8A

XXL #	locality	subspecies	back end of DCC’s	sex
#148	Yaoundé	*O. t. tetraspis*	is C-11	no data
#162	Campo Maan	*O. t. tetraspis*	is C-11	male
#164	Campo Maan	*O. t. tetraspis*	is C-11	no data
#166	Yaoundé	*O. t. tetraspis*	is C-11	female
#170	Yaoundé	*O. t. tetraspis*	is C-11	male
#172	Yaoundé	*O. t. tetraspis*	is C-11	female
#175	Campo Maan	*O. t. tetraspis*	is C-11	female
#180	Limbe	*O. t. tetraspis*	is C-11	no data
#183	Mundemba	*O. t. tetraspis*	is C-11	male
#184	Mundemba	*O. t. tetraspis*	is C-11	male

--- --- --- --- --- ten out of 33 have eleven double-crested caudals

Sub-table 6.8B

XXL #	locality	subspecies	back end of DCC’s	sex
#149	Yaoundé	*O. t. tetraspis*	is C-12	no data
#154	Yaoundé	*O. t. tetraspis*	is C-12	no data
#155	Yaoundé	*O. t. tetraspis*	is C-12	no data
#157	Yaoundé	*O. t. tetraspis*	is C-12	no data
#158	Yaoundé	*O. t. tetraspis*	is C-12	no data

#159	Yaoundé	*O. t. tetraspis*	is C-12	no data
#160	Campo Maan	*O. t. tetraspis*	is C-12	male
#161	Campo Maan	*O. t. tetraspis*	is C-12	female
#163	Campo Maan	*O. t. tetraspis*	is C-12	no data
#165	Campo Maan	*O. t. tetraspis*	is C-12	male
#167	Yaoundé	*O. t. tetraspis*	is C-12	female
#174	Yaoundé	*O. t. tetraspis*	is C-12	female
#176	Campo Maan	*O. t. tetraspis*	is C-12	no data
#182	Mundemba	*O. t. tetraspis*	is C-12	female

--- --- --- --- --- fourteen out of 33 have twelve double-crested caudals

Sub-table 6.8C

XXL #	locality	subspecies	back end of DCC’s	sex
#150	Yaoundé	*O. t. tetraspis*	is C-13	no data
#151	Yaoundé	*O. t. tetraspis*	is C-13	no data
#152	Yaoundé	*O. t. tetraspis*	is C-13	no data
#153	Yaoundé	*O. t. tetraspis*	is C-13	no data
#156	Yaoundé	*O. t. tetraspis*	is C-13	no data
#169	Yaoundé	*O. t. tetraspis*	is C-13	male
#171	Yaoundé	*O. t. tetraspis*	is C-13	female
#173	Yaoundé	*O. t. tetraspis*	is C-13	male

--- --- --- --- --- eight out of 33 have thirteen double-crested caudals

Sub-table 6.8D

XXL #	locality	subspecies	back end of DCC’s	sex
#181	Limbe	*O. t. tetraspis*	is C-14	no data

The sample from Cameroon (n=33) is the *Osteolaemus tetraspis tetraspis* Cope subspecies of African dwarf-crocodiles (COAST). In this coastal sample C-13 and C-14 also occur as the distal end of the double-crested caudal series. Only on sixteen animals was the sex known, but among these the sex of the animal appears to be random with regard to the number of its DCC’s.

Obviously twenty specimens (n=20) is not enough for characterizing the range of variation in DCC’s in an *Osteolaemus* Cope subspecies, because when n=33 the results are significantly different. Therefore it becomes clear that Robert Inger’s sample was too small. As a summary, the ranges of variation in the number of DCC’s are mapped in Figure 6.4 (below).

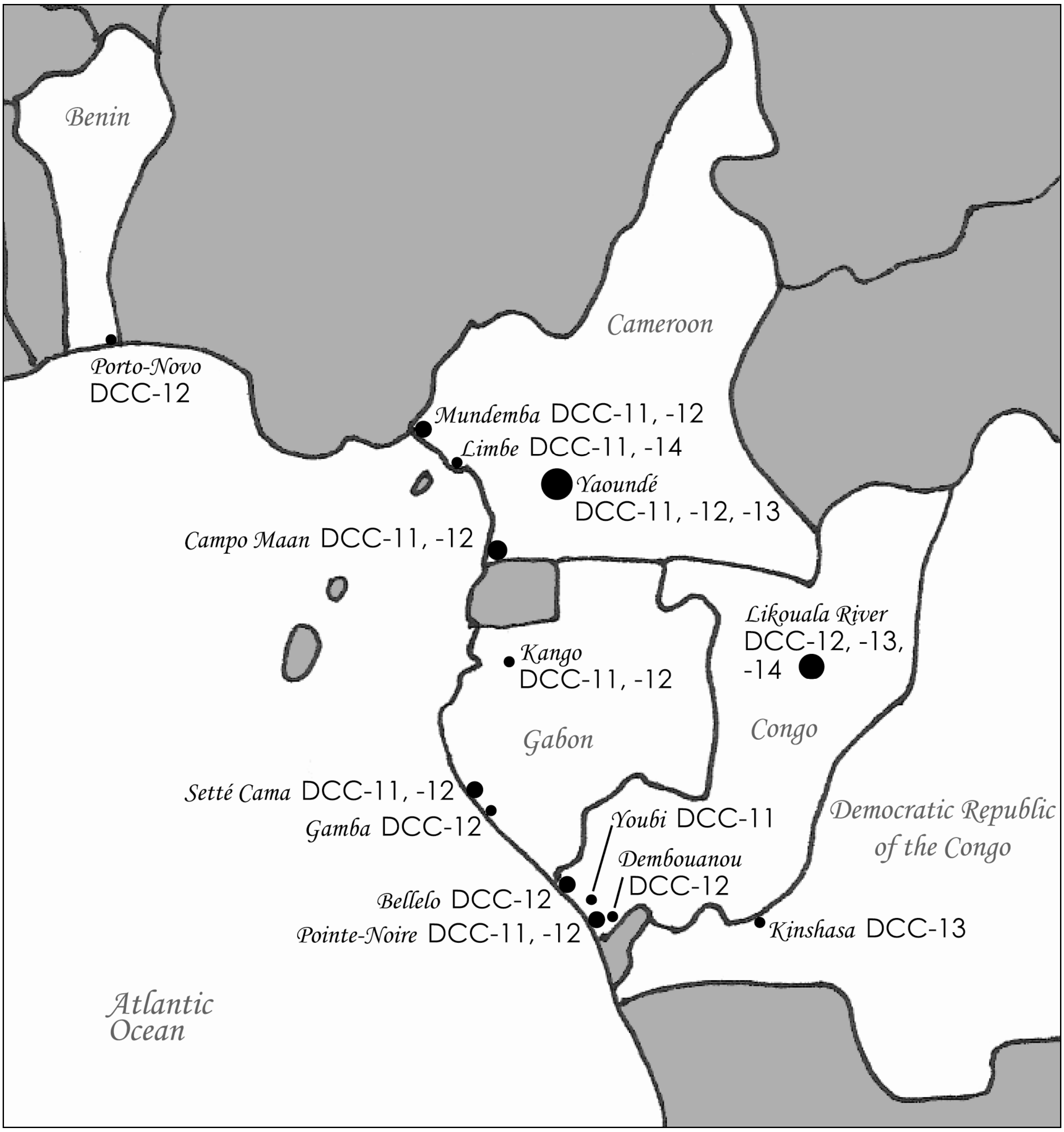


Figure 6.4 Double-crested caudal numbers plotted in terms of both sides of the taxonomic boundary between the supposed two subspecies of *Osteolaemus*

All of the observed double-crested caudal (DCC) numbers recorded in this new 2006-2007 field sample are plotted on this map. The local places Kinshasa (DRC) and Likouala (Congo-Brazzaville) represent the supposed subspecies *O. t. osborni*, and the other localities represent the supposed subspecies *O. t. tetraspis*.

The conclusion from the new DCC data is that Inger (1948) was correct about 11 DCC's occurring only in *O. t. tetraspis* meaning COAST zone samples as defined by C.I.T.E.S. However, the same geographic area produces results other than 11 DCC's very often, and thus the coastal subspecies actually broadly overlaps with *O. t. osborni* in the INTERIOR geography.

Having falsified Inger's hypothesis that DCC counts do not overlap between the two subspecies in *Osteolaemus*, the question remains about the characterizations of 10-12 DCC's in *O. t. tetraspis*, compared with 12-14 DCC's in the *O. t. osborni* subspecies, as asserted by Brazaitis (1973:79-80), Charette (1995:9 orange), and Fuchs (2006:132-137). In contrast to these three publications, the Zoer 2006-2007 *Osteolaemus* sample found that 13 and 14 DCC's can occur in *O. t. tetraspis*, and thus that the overlap between the two subspecies is greater than these authors had predicted.

As a general characterization, *Osteolaemus tetraspis tetraspis* has very rarely 10 DCC's (from Ross + Mayer, 1983), often 11 or 12 or 13 DCC's, and moderately rarely 14 DCC's, while the *O. t. osborni* subspecies has C-12 and C-13, and also C-14, but apparently not C-11 in the several small samples that have been studied. The double-crested caudals (DCC's) numbers in the literature are probably directly analogous to the DCC numbers in this thesis, because the theoretically problematic anterior and posterior ends of the DCC series are not a problem in the genus *Osteolaemus*. However, despite the high reliability of the data about DCC's, the diagnostic and predictive value of DCC numbers is of little practical utility, because of significant overlap between the two subspecies. Therefore, some additional dorsal armour characters must be tried, in the hope that one or more of them will provide the 100% diagnostic result that C.I.T.E.S. requires for identification of *Osteolaemus tetraspis* to subspecies.

The anterior edge of the tail is the posterior edge of the body. The sacro-caudal juncture (between C-1 and PC-1) and its relation to the posterior edge of the thighs was established in Chapter 5 (above), and now with PC-1 known, the dorsal armour on the body will be investigated below, starting with Chapter 7.

6.4 REVIEWING THE DOUBLE-CRESTED CAUDALS CHARACTER

In Chapter 6 the new data about the number of double-crested caudals (DCC's) falsified the prediction in Inger (1948:18) that no overlap in DCC numbers happens between the two subspecies, but this overlap at DCC's = 12 had already been predicted directly by Brazaitis (1973:79-80) and by Charette (1995:9 orange), and by Fuchs (2006:132-137), and indirectly by Wermuth + Fuchs (1983) and by Ross + Mayer (1983). What was unexpected was DCC's = 13 and DCC's = 14 happening in the COAST subspecies, making it harder than previously thought to identify any individual *Osteolaemus tetraspis* animal to subspecies by its number of double-crested caudal rows, unless it has only 11 or 10 of them, which currently appears to be diagnostic for the *O. t. tetraspis* subspecies as defined by C.I.T.E.S..

CHAPTER VII CONTINUOUS PRECAUDALS ARE TRANSVERSE ROWS BETWEEN TAIL AND NECK

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

7.1 INTRODUCTION

The prediction in Ross + Mayer's (1983:319, 326-327) text and table (reprinted below in Annexure A) was that *Osteolaemus tetraspis* Cope should have seventeen or eighteen transverse rows of precaudal scales located posterior to the cervico-thoracic juncture (CT-J). The CT-J is a transverse line between the 18th precaudal row (PC-18 is the most anterior thoracic row possible, when PC-18 is present) and the 19th precaudal row (PC-19 is the most posterior of the cervical pairs of nuchal scales, when PC-19 is present).

Not contradicting the above, when PC-18 is absent, then PC-17 is the most anterior of the thoracic rows. Similarly, when PC-19 is absent, the posterior of the two obligate transverse rows of nuchal scales on the neck becomes the most posterior of the nuchals, and also the distal end of the total cervical series (PO's and nuchals) on the neck of the African dwarf-crocodile. Note that both the Ross + Mayer (1983) data, and also the Zoer 2006-2007 expedition's data (unpublished), agree with each other that the Nile crocodile, *Crocodylus niloticus* Laurenti, can also have PC-18 and PC-17 exhibiting zero scales in contiguity; but in contrast, PC-17 is always present in the African slender-snouted crocodile, *Crocodylus cataphractus* Cuvier.

Similar to the format in earlier chapters, a comparison will be made here between specimens from the equatorial Atlantic coast nations, as compared with animals from far inland in central Africa. In this case, Benin, Cameroon, Gabon and Congo-Brazzaville (equatorial Atlantic coast) all got the label (place indication) "COAST" (meaning *O. t. tetraspis*), while in contrast, Congo-Brazzaville (Ubangi River region) and Zaïre-DRC got the label "INTERIOR" (meaning *O. t. osborni*).

7.2 METHODS

The 2006-2007 *Osteolaemus* expedition's field-protocol (for all crocodilian species encountered) requested that the precaudal transverse row of dorsal armour scales called PC-1 should be located first, and marked if possible by a small and colourful piece of tape, for later convenience. Similarly, PC-12 was also adorned with a little piece of sticky tape, to serve as a landmark. These two landmark rows (PC-1 and PC-12) are indicated in Figure 7.1 (below), where it becomes visually obvious that (although the vertebrae in the Crocodylia are normally numbered from the head toward the pelvis and tail) PC ("precaudal") numbers increase as they approach the head.

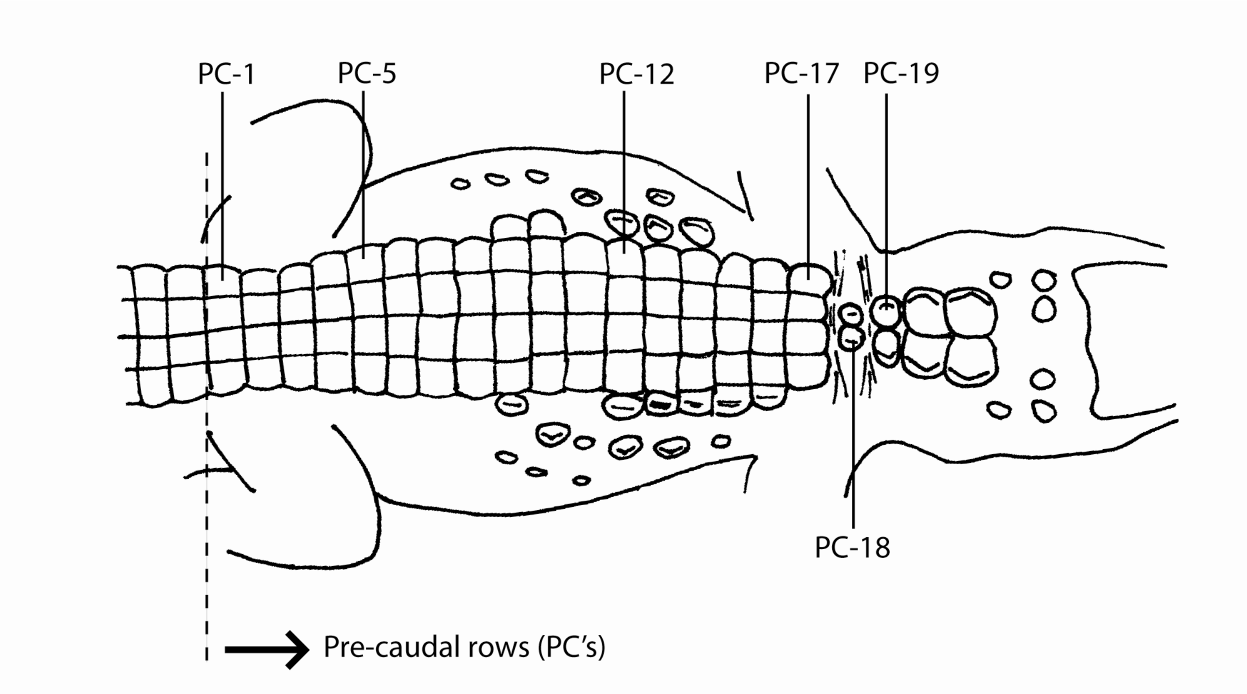


Figure 7.1 Counting precaudal rows (PC's) on the body

This female African dwarf-crocodile from Congo-Brazzaville at Likouala (= INTERIOR) has 19 precaudal rows posterior to its big and obligate nuchals. PC-18 is the most anterior thoracic row possible, and PC-19 is the most posterior of the cervical pairs of nuchal scales. Counting anteriorly away from the sacro-caudal juncture (= towards the head) all the way forward until the obligate nuchals, will result in the number of precaudal rows (PC's).

The number of precaudal rows was recorded of African dwarf-crocodiles from Congo-Brazzaville (equatorial Atlantic coast = COAST), Gabon COAST, Cameroon COAST, and Benin COAST, and also Congo-Brazzaville (Ubangi River region = INTERIOR), and Zaïre-DRC INTERIOR. The results about the number of precaudal rows in these African dwarf-crocodiles is presented below.

7.3 RESULTS

The Zoer 2006-2007 sample (n=68) of *Osteolaemus tetraspis* Cope falsifies (expands) the earlier Harvard University prediction (n=18), as shown in Table 7.1 (below) where PC-16 is sometimes the most anterior transverse row of thoracic scales, meaning that PC-17 has zero scales crossing the midline in contiguity, and PC-18 also has zero qualifying scales. When the two other living African crocodilian species are compared with *Osteolaemus*, the basic relationship from the Ross + Mayer (1983) data remains true. If PC-18 is present, the animal can be *Osteolaemus* Cope or *Croc. cataphractus* Cuvier, but not a Nile crocodile. If PC-17 is present, it could be any of the three. If PC-15 is the most anterior thoracic row, then the animal is *Crocodylus niloticus* Laurenti.

Table 7.1 Anteriormost thoracic precaudal row in the *Osteolaemus* field sample

Various possible conditions	frequency
18th precaudal row, PC-18, is present	58 out of 68
Alternatively PC-18 is absent	10 out of 68
Making PC-17 become the thoracic limit	7 out of 68
But PC-17 (and also PC-18) can be absent	3 out of 68
Making PC-16 become the anterior limit of the dorsal body armour three times (n=68)	3 out of 68

On almost all of the African dwarf-crocodile specimens in the Zoer 2006-2007 sample, except for ten animals, the 18th precaudal row is present. The only other living African crocodilian that can be missing PC-18 and PC-17 is the Nile crocodile, *Crocodylus niloticus* Laurenti, which in extreme cases can be missing PC-16 also.

When the various possibilities for the most anterior transverse row of thoracic scales in Table 7.1 are arranged as a bar graph in Figure 7.2 for the same 68 African dwarf-crocodiles, it is easy to see that the Ross + Mayer (1983) prediction was close to the truth, but the Harvard University sample was too small, and with n=18, there were no examples in the 1983 study that had fusions among the obligate nuchals. If the fusions and compounding (creating stiffness) in the cervical shield is in any way related to the details of compensating flexibility in the thoracic armour, it could help to explain this apparently formerly unknown character state where the 16th precaudal transverse row of scales on the body (PC-16) is sometimes bordered anteriorly by a major space of bare skin.

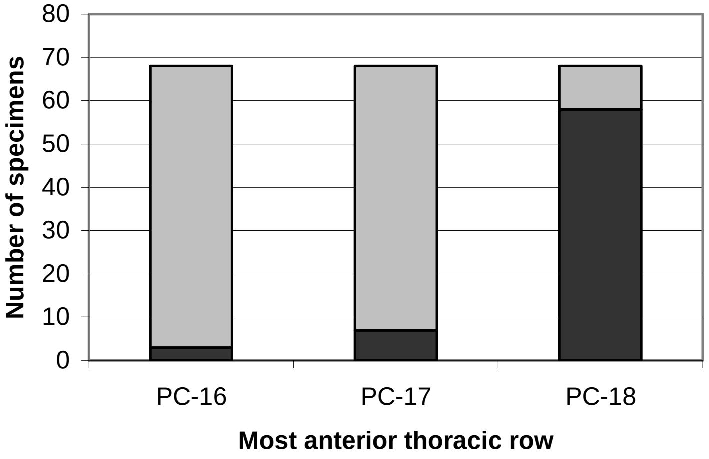


Figure 7.2 Frequency of being the most anterior thoracic row

The African dwarf-crocodile species has the 18th precaudal row (PC-18) present in the vast majority of this sample (58 out of 68) from Congo-Brazzaville COAST, Gabon, Cameroon and Benin near the Atlantic Ocean (all COAST), and Brazzaville and Kinshasa cities as a region (both INTERIOR), and the Ubangi River in the Congo-Brazzaville northeastern INTERIOR, and presumably also across the river in Zaïre-DRC in the Ubangi River drainage (INTERIOR). In seven (7) out of 68 cases the most anterior thoracic row is PC-17, and in three (3) out of 68 cases the most anterior row is PC-16.

Note that all of the data in Section 7.3 disregards the presence or absence of PC-19 on the neck, because the Ross + Mayer (1983) definition was that only anatomically true thoracic, lumbar and pelvic transverse rows are included in the body armour (PC-18 is the anterior end of the body). However, the Ross + Mayer (1983) study covered all 21 of the living crocodilian species, and *Osteolaemus tetraspis* Cope was just one of many. The 1983 model from the Museum of Comparative Zoology was technically correct about PC-19 being excluded from the African dwarf-crocodile's thoracic section because the ribs of the 19th precaudal vertebral centrum do not contact the sternum (sources like A.S. Romer's book Osteology of the Reptilia) and are thus cervical, while the ribs associated with the centrum of the 18th precaudal vertebra do actually make contact with the sternum, and are thus thoracic.

The skeletal distinction between cervical vertebrae and thoracic vertebrae is a case of drawing a line through a cline. The ribs of the 19th precaudal centrum almost reach the sternum in all crocodilians, and the ribs of the 18th precaudal centrum just barely reach the sternum. The transition is extremely gradual, and is a specialist's study. The Ross + Mayer (1983) cervico-thoracic juncture (CT-J) for the crocodilian order was accepted as true in the early 1980’s by Dr. Ernest Edward Williams, Agassiz Professor of vertebrate anatomy, Harvard University.

The dorsal view illustration of the thoracic and cervical scales on the African dwarf-crocodile in Ross + Mayer (1983:fig. 9-A) was an extreme of recorded variation, explained on page 319 of the n=18 report from the Museum of Comparative Zoology as “In a single specimen (Fig. 9A), only one row of two small elements occurs between PC-17 and the two large rows of the cervical shield.” Thus it was known to be possible for *Osteolaemus tetraspis* Cope to have a considerable space of unarmoured skin widely separating the anterior edge of the thoracic armour from the posterior edge of the cervical shield (and Table 7.1 and also Figure 7.2 in this thesis confirm it). However, most of the time the thoracic armour in the genus *Osteolaemus* Cope is almost continuous with the cervical armour, especially when (fusions aside) all six of the possible nuchal scales are present, making three transverse rows in the cervical shield, each row with a pair of nuchal scales in it. For details and illustrations about nuchal scales, please see Chapter 3 (above), including the frequency of occurrence of transverse row PC-19 on the neck of the African dwarf-crocodile.

For wildlife biologists and others working with specimens, or working from photographs, the majority of *Osteolaemus tetraspis* Cope will appear (at first glance) to lack transverse strips of unarmoured skin in the cervico-thoracic juncture (CT-J) region. Thus, the dorsal armour on the body can appear to continue all the way anterior to the start of the really big nuchals. These animals are usually individuals on which both PC-18 and PC-19 are present, but it is probably possible to delete one row (PC-18 or alternatively PC-19) and have other adjacent row lengths (along the long-axis of the crocodile) compensating for the loss of PC-18 or PC-19 by themselves enlarging enough that the thoracic scalation on the body appears to be continuous with the cervical shield. In other words, the loss of one row can create a theoretical space of unarmoured skin that is secondarily filled by expansion of its neighboring transverse rows.

The “fold” of skin separating the posterior obligate pair of nuchals from PC-19 in the Ross + Mayer (1983:319) *Osteolaemus tetraspis* species account is present in 100% of the Zoer 2006-2007 sample (n=68) of African dwarf-crocodiles. This transverse strip of skin was known (and obligate), and the frequent occurrence of a second and optional “fold” between PC-19 and PC-18 (or PC-17 if PC-18 is missing, etc. = PC-17 can be missing too) was also expected (see details and pictures in Chapter 3 above). However, the presence of transverse strips of bare and flexible skin between PC-18 and PC-17, and also between PC-

17 and PC-16 are new discoveries. If these additional “folds” of skin have ever appeared in published photographs, the phenomenon was not discussed.

7.3.1 Degree of cervico-thoracic separation, with implications assessed

The immediate importance of the unexpected “folds” between PC-18 and PC-17, and also between PC-17 and PC-16, is that the instructions in the Ross + Mayer (1983) paper say that, starting at the back edge of the pelvis at the sacro-caudal juncture (SC-J), the precaudal rows are a continuous series all the way to the cervico-thoracic juncture (CT-J), or even beyond the CT-J in some taxa (*Tomistoma* and *Gavialis*, for example). Thus, if the instructions in Ross + Mayer (1983) are followed literally, the results in the 2006-2007 African dwarf-crocodile sample (n=68) would be those in Table 7.2 below, where PC-19 is considered available.

Table 7.2 Continuous precaudal rows in the 2006-2007 sample (n=68)

No fold of skin until anterior edge of row #	specimens
16th precaudal row (PC-16) is the anteriormost continuous	4 out of 68
17th precaudal row (PC-17) is the anteriormost continuous	20 out of 68
18th precaudal row (PC-18) is the anteriormost continuous	38 out of 68
19th precaudal row (PC-19) is the anteriormost continuous	6 out of 68

The continuous series of precaudal rows in the 2006-2007 sample of African dwarf-crocodiles are considerably variable. Warning: these results are not to be confused with Table 7.1 and Figure 7.1 above (the same sample, but with different definitions of the “continuous” scalation character). Rather, this Table 7.2 data allows additional thoracic rows to occur anterior to PC-16 in four cases, and allows PC-18 to be present when the fold of skin is at the anterior edge of PC-17 in 20 cases. In this table, 38 cases exhibited no folds of skin posterior to PC-18, and similarly there were no folds of skin posterior to PC-19 in six African dwarf-crocodiles. These last five individuals contradict the Ross + Mayer (1983:319) prediction for *Osteolaemus tetraspis* that “Anterior to PC 18 there is a fold of skin...” before the cervical-shield begins. See Ross + Mayer (1983), reprinted below in Annexure A.

In detail, one female *Osteolaemus* from Zaïre-DRC had a fold of flexible skin at the anterior edge of PC-16, and also had a fold at the anterior edge of PC-17, and a fold between PC-17 and PC-18, and an additional fold between PC-18 and PC-19, and thus exhibited all four of the optional folds, and she had the obligate fold between PC-19 and the enlarged nuchals, creating a total of five (5) transverse spaces of flexible skin in the cervico-thoracic juncture (CT-J) region in its most inclusive sense. This single individual is #XXL-17 from Zaïre-DRC INTERIOR at Kinshasa.

Also, six dwarf-crocodiles from Congo-Brazzaville exhibited 17 continuous precaudal rows, and all six of these *Osteolaemus* had PC-18 and PC-19 present. They are XXL-116 (Congo-Brazzaville INTERIOR at Likouala, sex unknown); XXL-121 (Congo-Brazzaville INTERIOR at Likouala, male); XXL-106 (Congo-Brazzaville COAST at Bellelo, female); XXL-113 (Congo-Brazzaville INTERIOR at Likouala, sex unknown); XXL-123 (Congo-Brazzaville INTERIOR at Likouala, female); and XXL-124 (Congo-Brazzaville COAST at Youbi, male). Both sexes are present in this sample of six animals that have the body armour in a sense "continuous" across the cervico-thoracic juncture, and reaching the really big nuchals. Note that Atlantic coastal localities and also some interior (Ubangi River drainage) animals are represented in this sample, and thus both of the C.I.T.E.S. recognized subspecies can exhibit this remarkably continuous dorsal armour condition.

Similarly, two *Osteolaemus* specimens from Congo-Brazzaville (one Atlantic Ocean coastal and the other from an "interior" Ubangi River drainage locality), and also seven dwarf-crocodiles from Cameroon, all had 17 continuous precaudal rows, and had PC-18 present. This group of nine African dwarf-crocodiles (with PC-1 to PC-18 present, but PC-19 missing) are XXL-105 (Congo-Brazzaville COAST at Pointe-Noire, sex unknown); #XXL-112 (Congo-Brazzaville INTERIOR at Likouala, female); XXL-148, #153, #156, and #163 (Cameroon, sex unknown); XXL-171, #172, and #174 (Cameroon, females), with no known-males among these nine individuals. Note that the Likouala River was sampled indirectly through a bushmeat market downriver from "Likouala", with locality information obtained in Brazzaville (considered reliable), and known in the literature. For example, Thorbjarnarson + Eaton work (2003:7, 2004:237) said that dwarf-crocodiles captured south and west of the sharp bend toward the east in the Ubangi River get sent alive downriver, on the Ubangi and then on the Congo River itself, to the Brazzaville market. These factors make Likouala qualify as INTERIOR and thus the Likouala River sample represents the Ituri Forest of Zaïre-DRC special subspecies, *Osteolaemus tetraspis osborni* (Schmidt) recognized by C.I.T.E.S. today.

On the dorsal surface of the African dwarf-crocodile, the unexpected optional "folds" (= thin transverse strips) of flexible skin that occur in some cases inside of the otherwise "continuous" (= uninterrupted by spaces of unarmoured skin) precaudal rows in the series starting at the sacro-caudal juncture (SC-J) with PC-1, and continuing through PC-16, PC-17, PC-18, and even sometimes PC-19, do not count (= do not constitute a break in the continuous series in this one species only). They can be ignored in dwarf-crocodiles in Africa, because the precaudal series of transverse dorsal-armour rows in *Osteolaemus tetraspis* Cope (on a superficial and first-glance level) appears to cross the cervico-thoracic juncture (CT-J) and continue onto the base of the neck. These surprising details (see above within this section) have required the old definition of “continuous” precaudal rows to be rewritten and specially modified for the genus *Osteolaemus* Cope (here in Subsection 7.3.1, for application in Subsection 7.3.2 below).

Before abandoning (postponing for further study and special publication) the subject of optional and unexpected extra transverse “folds” of interscale skin located inside of the African dwarf-crocodile’s thoracic zone, there is the theoretical possibility that their frequency of occurrence can be correlated with geography or sex. However, both sexes (Subsection 7.3.1 above) exhibit the phenomenon, and locality data includes animals from both sides of the subspecies boundary, as will be shown in Table 7.3 (below) with the two taxa of *Osteolaemus tetraspis* subspecies indicated.

Table 7.3 Geographic distribution of specimens with folds among their thoracic rows

Folds on anterior edges of	XXL #	locality data	taxon
PC-16, PC-17, and PC-18	#17	Zaïre-DRC at Kinshasa	*O.t.o.*
PC-17 and PC-18	#105	Congo-Brazzaville at Pointe-Noire	*O.t.t.*
PC-17 and PC-18	#106	Congo-Brazzaville at Bellelo	*O.t.t.*
PC-17 and PC-18	#112	Congo-Brazzaville at Likouala	*O.t.o.*
PC-17 and PC-18	#113	Congo-Brazzaville at Likouala	*O.t.o.*
PC-17 and PC-18	#116	Congo-Brazzaville at Likouala	*O.t.o.*
PC-17 and PC-18	#121	Congo-Brazzaville at Likouala	*O.t.o.*
PC-17 and PC-18	#123	Congo-Brazzaville at Likouala	*O.t.o.*
PC-17 and PC-18	#124	Congo-Brazzaville at Youbi	*O.t.t.*
PC-17 and PC-18	#134	Gabon at Setté Cama	*O.t.t.*
PC-17 and PC-18	#148	Cameroon at Yaoundé	*O.t.t.*
PC-17 and PC-18	#153	Cameroon at Yaoundé	*O.t.t.*
PC-17 and PC-18	#156	Cameroon at Yaoundé	*O.t.t.*
PC-17 and PC-18	#163	Cameroon at Campo Maan	*O.t.t.*
PC-17 and PC-18	#171	Cameroon at Yaoundé	*O.t.t.*
PC-17 and PC-18	#172	Cameroon at Yaoundé	*O.t.t.*
PC-17 and PC-18	#174	Cameroon at Yaoundé	*O.t.t.*

O.t.t. = Osteolaemus tetraspis tetraspis Cope. All COAST localities are *Osteolaemus tetraspis tetraspis* Cope. Similarly, the abbreviation *O.t.o. = Osteolaemus tetraspis osborni* (Schmidt). The two INTERIOR locations (Congo-Brazzaville at Likouala and Zaïre-DRC at Kinshasa) are the *Osteolaemus tetraspis osborni* (K.P. Schmidt) subspecies. Note that the nation of Benin is not represented in this table, because that individual specimen lacked transverse folds in its thoracic scalation.

In some animals PC-19 is present (together with PC-18). The presence of PC-19 is possibly correlated with thoracic folds of flexible skin. In Table 7.4 (below) the presence or absence of PC-19 is presented together with the presence or absence of a fold of skin in between PC-18 and PC-19 in this sample.

Table 7.4 Presence of PC-19 in the Zoer 2006-2007 sample (n=68)

Questions about PC-19 and folds of skin	number of specimens
PC-19 is present?	45
PC-19 is not present?	23
Fold of skin between PC-18 and PC-19?	62
No fold of skin between PC-18 and PC-19?	6

This table presents the number of *Osteolaemus* in this sample which have PC-19 present or absent. Additionally, this table shows that the majority of the animals (62) have a fold of skin posterior to PC-19, as opposed to six (6) African dwarf-crocodiles without a fold of skin in between PC-18 and PC-19.

The six African dwarf-crocodiles without a fold of skin posterior to PC-19 are sex-data examined in Table 7.5 below. These animals contradict Ross + Mayer (1983), because anterior to PC-18 there is no fold of skin before reaching a row of two small elements (being PC-19), followed anteriorly by an obligate fold of skin, and then two rows of two large elements each. These latter two transverse rows are the obligate nuchals.

Table 7.5 Locality and sex data for animals with PC-19 present, without a fold of flexible skin between it and PC-18

XXL specimen #	sex	place of origin	subspecies
#109	male	Congo-Brazzaville at Bellelo	*tetraspis*
#119	male	Congo-Brazzaville at Likouala	*osborni*
#128	male	Congo-Brazzaville at Pointe-Noire	*tetraspis*
#149	no sex	Cameroon at Yaoundé	*tetraspis*
#152	no sex	Cameroon at Yaoundé	*tetraspis*
#155	no sex	Cameroon at Yaoundé	*tetraspis*

The animals without a fold of flexible skin between PC-18 and PC-19 are from both coastal and inland localities (Congo-Brazzaville and Cameroon). Sex is known for three of these animals, and they happen to be male individuals from Congo-Brazzaville.

The cervico-thoracic separation appears to be rather random in animals from coastal localities, as compared with *Osteolaemus* from the inland zones in this 2006-2007 African dwarf-crocodile sample. For a closer look at the "folds" of skin located between the thoracic rows, and also the number of precaudal rows, the results will be presented sample by sample in Subsection 7.3.2 below.

7.3.2 Variation in the precaudal series of transverse rows of dorsal-armour posterior to the obligate nuchals reviewed for geographic and sexual variation, sample by sample

The special *Osteolaemus* redefined series of precaudal transverse-rows of dorsal scales can be continuous from PC-1 to PC-19, when there are no dorsal-armour rows deleted at the cervico-thoracic juncture (CT-J). Table 7.6 summarizes the total variation in the Zoer 2006-2007 African dwarf-crocodile sample (n=68).

Table 7.6 The most anterior thoracic row is variable

Scale-row #	number of specimens
Precaudal row PC-16	3 out of 68 African dwarf-crocodiles
Precaudal row PC-17	7 out of 68 African dwarf-crocodiles
Precaudal row PC-18	58 out of 68 African dwarf-crocodiles

The most anterior thoracic row is PC-18 in 58 out of 68 African dwarf-crocodiles in the 2006-2007 sample. The 19th precaudal row, present in 45 out of 68 animals, is not included in this table, because PC-19 is cervical and not thoracic. The number of thoracic rows will be examined nation by nation, below.

The smallest sample in the 2006-2007 field-data collection was a single fairly big animal in captivity in the Atlantic coastal city of Porto Novo in the nation of Benin, believed to be local. By geography, this African dwarf-crocodile must be *Osteolaemus tetraspis tetraspis* Cope, because it is a Gulf of Guinea (Atlantic Coast) animal. Table 7.7 shows that this individual has the most commonly encountered pattern of precaudal armour posterior to the “obligate” (the two pairs of big square bony scales of the cervical shield) nuchals.

Table 7.7 The nation of Benin sample is one animal

Specimen #	row behind obligates	sex	locality
XXL-185	PC-18 is most anterior	no sex	Porto Novo

This animal from Benin at Porto Novo has eighteen (18) thoracic precaudal rows posterior to the obligate nuchals. This individual represents the Atlantic Ocean coastal subspecies *Osteolaemus tetraspis tetraspis* Cope.

Benin is immediately west of Nigeria (also the *Osteolaemus tetraspis tetraspis* subspecies), and the nation of Benin was as far west along the Gulf of Guinea coast as the

Zoer 2006-2007 expedition gathered data on African dwarf-crocodiles. The much larger sample from the nation of Cameroon in Table 7.8 is also all the subspecies *Osteolaemus tetraspis tetraspis* Cope, because all of the collecting stations (localities sampled) are in direct Atlantic Ocean coastal drainages (local rivers), as opposed to the Ubangi River drainage of the Congo River system.

Table 7.8 The large sample from Cameroon (number of PC rows present)

XXL #	1st row behind obligate nuchals	sex	locality
#160	PC-16 is the most anterior	male	Campo Maan
--- --- ---	--- --- --- --- --- --- --- ---	--- --- ---	--- --- --- ---
#157	PC-17 is the most anterior	no sex	Yaoundé
#158	PC-17 is the most anterior	no sex	Yaoundé
#171	PC-17 is the most anterior	female	Yaoundé
#184	PC-17 is the most anterior	male	Mundemba
--- --- ---	--- --- --- --- --- --- --- ---	--- --- ---	--- --- --- ---
#148	PC-18 is the most anterior	no sex	Yaoundé
#149	PC-18 is the most anterior	no sex	Yaoundé
#150	PC-18 is the most anterior	no sex	Yaoundé
#151	PC-18 is the most anterior	no sex	Yaoundé
#152	PC-18 is the most anterior	no sex	Yaoundé
#153	PC-18 is the most anterior	no sex	Yaoundé
#154	PC-18 is the most anterior	no sex	Yaoundé
#155	PC-18 is the most anterior	no sex	Yaoundé
#156	PC-18 is the most anterior	no sex	Yaoundé
#159	PC-18 is the most anterior	no sex	Yaoundé
#161	PC-18 is the most anterior	female	Campo Maan
#162	PC-18 is the most anterior	male	Campo Maan
#163	PC-18 is the most anterior	no sex	Campo Maan
#164	PC-18 is the most anterior	no sex	Campo Maan
#165	PC-18 is the most anterior	male	Campo Maan
#166	PC-18 is the most anterior	female	Yaoundé
#167	PC-18 is the most anterior	female	Yaoundé
#169	PC-18 is the most anterior	male	Yaoundé
#170	PC-18 is the most anterior	male	Yaoundé
#172	PC-18 is the most anterior	female	Yaoundé
#173	PC-18 is the most anterior	male	Yaoundé
#174	PC-18 is the most anterior	female	Yaoundé

#175	PC-18 is the most anterior	female	Campo Maan
#176	PC-18 is the most anterior	no sex	Campo Maan
#180	PC-18 is the most anterior	no sex	Limbe
#181	PC-18 is the most anterior	no sex	Limbe
#182	PC-18 is the most anterior	female	Mundemba
#183	PC-18 is the most anterior	male	Mundemba

The majority of animals from Cameroon have eighteen (18) thoracic precaudal rows. Note that Cameroon is COAST (*Osteolaemus tetraspis tetraspis* Cope), and that only thoracic PC rows are considered (PC-19 is cervical and not thoracic) in this table. One male specimen from Campo Maan has sixteen (16) continuous precaudal rows. Similarly seventeen (17) precaudal rows also occur at a low frequency, being represented by four individuals.

The most common outcome in animals from Cameroon is eighteen (18) thoracic precaudal rows, together with some lower numbers of precaudal rows. Therefore, in a bigger sample, some variation in results can be generally expected. The sex ratio (when known) appears random about which sex has short (= PC-16 and PC-17) or which sex has common (= PC-18) numbers of thoracic PC rows.

The Zoer 2006-2007 expedition sample from Gabon is all from Atlantic Ocean coastal situations, as compared with the interior of the continent (the Congo and Ubangi drainage). Thus the whole sample is clearly *Osteolaemus tetraspis* Cope, and also, assuming that Schmidt’s subspecies is real, the Gabon sample of eight (8) African dwarf-crocodiles are topotypes of *Osteolaemus t. tetraspis*, by definition. In theory, because they are functionally adjacent to each other, there should be little difference between the Cameroon sample (Table 7.8 above), compared with the Gabon sample in Table 7.9 below.

Table 7.9 Gabon nation (number of PC rows present)

XXL #	1st row behind obligate nuchals	sex	locality
#132	PC-16 is the most anterior	male	Kango
#139	PC-16 is the most anterior	no sex	Gamba
--- --- ---	--- --- --- --- --- --- --- ---	--- --- ---	--- --- --- --- ---
#130	PC-17 is the most anterior	female	Kango
--- --- ---	--- --- --- --- --- --- --- ---	--- --- ---	--- --- --- --- ---
#134	PC-18 is the most anterior	female	Setté Cama
#135	PC-18 is the most anterior	female	Setté Cama
#136	PC-18 is the most anterior	male	Setté Cama
#137	PC-18 is the most anterior	male	Setté Cama
#138	PC-18 is the most anterior	female	Setté Cama

Gabon at the coastal Ogowe River is the type locality of *Osteolaemus tetraspis tetraspis* Cope (= COAST). Three animals (XXL-130, #132, and XXL-139) have low (16-17) numbers in their thoracic PC series. All five animals from the Setté Cama locality have eighteen thoracic PC rows.

The Cameroon and Gabon samples both have at least three animals with less than eighteen (18) thoracic precaudal rows. These eight African dwarf-crocodiles with the shortest series of thoracic transverse PC rows in the 2006-2007 sample are fairly equally either male or female. The Benin individual has, like the majority of both Cameroon and Gabon, eighteen (18) thoracic PC rows, which is the most commonly encountered pattern of thoracic precaudal rows. This result of few animals with 16-17 rows, compared with many animals with 18 rows, resembles the graph in Figure 7.2 (above).

Because it is again functionally adjacent to the previous nations, the expectation is that the coast of Congo-Brazzaville will show the same pattern as above. The results of this other coastal locality are displayed in Table 7.10 below. There is a possibility of geographic variation between COAST (*Osteolaemus tetraspis tetraspis*) and INTERIOR (*Osteolaemus tertaspis osborni*). Therefore, to save space, the Congo-Brazzaville INTERIOR specimens are included in Table 7.10 as well. The second INTERIOR locality (Zaïre-DRC at Kinshasa) will be discussed separately, later.

Table 7.10 Congo-Brazzaville (number of PC rows present)

XXL #	1st row behind big nuchals	sex	locality
#104	PC-17 is the most anterior	no sex	Pointe-Noire COAST
#125	PC-17 is the most anterior	male	Dembouanou COAST
--- --- ---	--- --- --- --- --- ---	--- --- ---	--- --- --- --- --- ---
#105	PC-18 is the most anterior	no sex	Pointe-Noire COAST
#106	PC-18 is the most anterior	female	Bellelo COAST
#107	PC-18 is the most anterior	female	Bellelo COAST
#108	PC-18 is the most anterior	male	Bellelo COAST
#109	PC-18 is the most anterior	male	Bellelo COAST
#110	PC-18 is the most anterior	male	Likouala INTERIOR
#111	PC-18 is the most anterior	male	Likouala INTERIOR
#112	PC-18 is the most anterior	female	Likouala INTERIOR
#113	PC-18 is the most anterior	no sex	Likouala INTERIOR
#114	PC-18 is the most anterior	no sex	Likouala INTERIOR
#115	PC-18 is the most anterior	no sex	Likouala INTERIOR
#116	PC-18 is the most anterior	no sex	Likouala INTERIOR
#117	PC-18 is the most anterior	no sex	Likouala INTERIOR
#118	PC-18 is the most anterior	male	Likouala INTERIOR
#119	PC-18 is the most anterior	male	Likouala INTERIOR
#120	PC-18 is the most anterior	male	Likouala INTERIOR
#121	PC-18 is the most anterior	male	Likouala INTERIOR
#122	PC-18 is the most anterior	female	Likouala INTERIOR
#123	PC-18 is the most anterior	female	Likouala INTERIOR
#124	PC-18 is the most anterior	male	Youbi COAST
#126	PC-18 is the most anterior	no sex	Pointe-Noire COAST
#127	PC-18 is the most anterior	no sex	Pointe-Noire COAST
#128	PC-18 is the most anterior	male	Pointe-Noire COAST

The occurrence of PC-17 at the coast is rare and could occur elsewhere in larger samples. Results are COAST = PC-17, and PC-18; and results are INTERIOR = PC-18. The most frequent occurrence in the species is PC-18 (see Table 7.8, above), and it is most frequent in both of the C.I.T.E.S. subspecies zones of geography.

The sex ratio in Congo-Brazzaville appears random about which sex has a low (= PC-17), common (= PC-18), or high (= PC-19) number of continuous PC rows. This is the same pattern of variation that was observed in animals from Gabon and Cameroon, and also the one animal from Benin. Similar to the small Benin sample, only one African dwarf-crocodile from Zaïre-DRC nation is presented in Table 7.11 (below). Note that the city of Kinshasa has a bushmeat market, and thus the Zaïre-DRC sample lacks precise locality data. However, the nation is probably correct, and its classification as an "interior" locality (= C.I.T.E.S. ecology) is reasonably certain (the living specimen was thought to be local Zaïre-DRC by the person who purchased it decades ago, and transported it to southern Africa, where it was later examined in 2006 at Hoedspruit in the nation of South Africa).

Table 7.11 The most anterior thoracic row in animals from Zaïre-DRC

XXL #	1st row behind big nuchals	sex	locality
#17	PC-18 is the most anterior	female	Kinshasa INTERIOR

This female from Zaïre-DRC at Kinshasa has eighteen (18) thoracic precaudal rows. Note that the geographic distribution of *Osteolaemus tetraspis osborni* (Schmidt) was originally believed by H. Lang (the collector of the *Osteoblepharon osborni* type series) to reach "Stanley Pool" in the immediate vicinity of the city of Kinshasa today.

Posterior to the posterior obligate pair of large rectangular nuchal scales, the transverse row PC-19 is sometimes present, and in contrast it is also sometimes absent. This generality agrees with Ross + Mayer (1983:319-320), who said that PC-19 is normally present as two scales, while illustrating a specimen from Liberia nation (in the COAST category) that lacks PC-19 completely (see Ross + Mayer's figure 9-A in Annexure A, below).

The presence or absence of PC-19 does not appear to be influenced by the sex of the African dwarf-crocodile. Similarly, the anteriormost thoracic row, such as PC-18 and PC-17, does not correlate with sex. The number of transverse rows, and also the number of scales within each row, do not change as the baby crocodile grows to adult size (Ross + Mayer 1983:313) Thus, neither size nor sex explain the observed variation. Therefore, geography deserves a visual review, in the hope that an "ecological" (defined by C.I.T.E.S.) pattern in precaudal rows (PC's) will emerge on the map in Figure 7.3 (below).

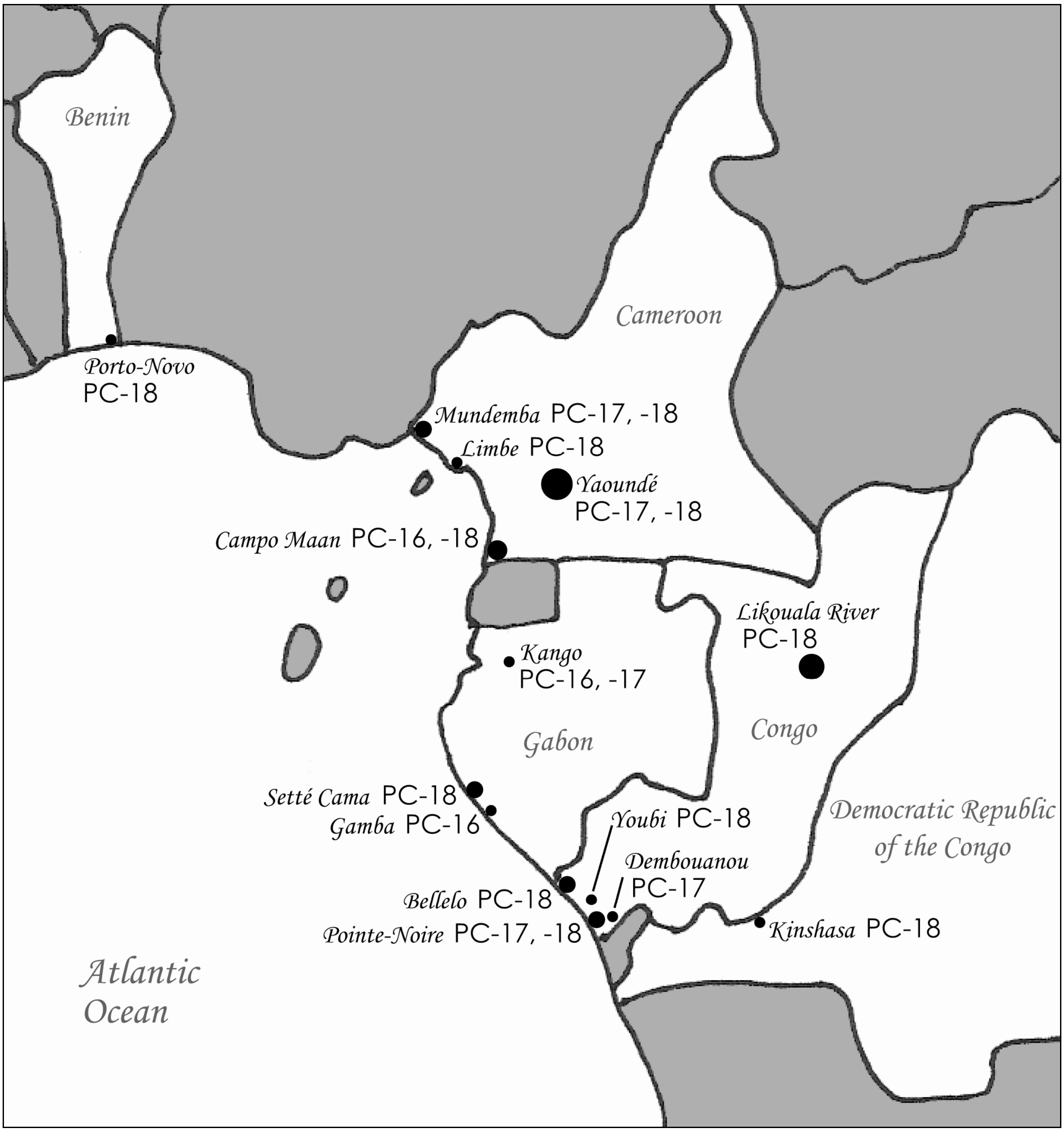


Figure 7.3 Precaudal row numbers plotted in terms of both sides of the taxonomic boundary between the supposed two subspecies of *Osteolaemus*

All of the anteriormost precaudal (PC) results recorded in this 2006-2007 field-sample, when PC-19 is excluded from consideration, are plotted on this map. Thus, this is the precaudal series on the body that Ross + Mayer (1983) employed for all of the living crocodilian species. The local places Kinshasa (DRC) and Likouala (Congo-Brazzaville) represent the supposed subspecies *O. t. osborni*, and the other localities represent the supposed subspecies *O. t. tetraspis*.

In the next chapter a new character will be introduced. The two kinds of dorsal scalation characters from Chapters 6 and 7 will be added together into a single scale-count. The exact method used and its advantages for scientists counting dorsal scales will be detailed.

7.4 REVIEWING THE PRECAUDAL ROWS BETWEEN THE TAIL AND THE OBLIGATE NUCHALS

In *Osteolaemus tetraspis* as an individual crocodilian species, the number of continuous precaudal (PC) transverse rows of dorsal armor on the body involves variable small transverse spaces of flexible skin, and often more than one of these minor interruptions in the otherwise “continuous” series of transverse body-rows is encountered. Therefore the Ross + Mayer (1983) definition of the word “continuous” has here been modified to not only ignore the unexpected thoracic interruptions, but to also ignore the predicted yet often inconspicuous cervico-thoracic space, and to thus bring PC-19 (on the neck) into this scale-count as an *Osteolaemus* special character. This is partly because all attempts to correlate the number and physical placement of thin and unarmored skin-folds with the sex of the individual African dwarf-crocodiles failed. Further, geography (as defined by the traditional C.I.T.E.S. subspecies distribution maps) was also disappointing, and even the presence or absence of an obvious cervico-thoracic juncture (CT-J) did not consistently discriminate between what C.I.T.E.S. calls *Osteolaemus tetraspis tetraspis* Cope and *Osteolaemus tetraspis osborni* (K.P. Schmidt).

In the first half of Chapter 7 it was found that transverse thin folds (spaces) of flexible skin located between various anterior transverse body-rows of PC scales, and also the unarmored thin transverse space located between the neck and the thoracic part of the body (at the CT-J), are both of little utility as a character (or characters) for distinguishing subspecies taxa in *Osteolaemus tetraspis* Cope. Therefore, in the second half of Chapter 7 it was alternatively hoped (a second hypothesis) that the number of actual transverse rows of scales physically present, and their identifications of the animals to either sex or geography, would perhaps correlate strongly. However, again individual variation was so significant that the predictive power of these characters does not achieve the 100% certainty required for C.I.T.E.S. enforcement.

It appears that, in *Osteolaemus* as a genus, the PC counts are not reliably predictive at the subspecies level. Variation in precaudal scale-rows (including PC-19 on the neck) is greater than was expected from the Ross + Mayer (1983) paper, but the new results appear to mean little or nothing, even when the sample size (n=68) is the largest ever assembled for taxonomic science in this crocodilian species. What is remarkable about the African dwarf-crocodile is that all of the variations in continuous PC's (including PC-19) appear to physically cover and protect the animal's neck to the same exact amount, when viewed in a functional sense. In other words, the bodies and necks of all *Osteolaemus* look very much the same at first glance, and counting the rows, and analyzing the folds, though possible, does not significantly alter the conclusion that the number of "continuous" (either the Ross + Mayer definition, or the new special *Osteolaemus* definition) precaudal rows does not reliably discriminate between the two C.I.T.E.S. taxa as they have been mapped and defined (as mostly whole nations like Cameroon and Gabon) in the past.

CHAPTER VIII EXPERIMENT COMBINING THE DORSAL BODY WITH PART OF THE NECK AND THE TAIL: THE PERMIT-FREE COUNT

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

8.1 INTRODUCTION

The number of double-crested caudals (DCC's) has already been discussed and tabulated in Chapter 6 (above), and the number of precaudal rows (PC's) on the body and on the base of the neck was presented in Chapter 7 (above), so now the two kinds of dorsal scalation characters from Chapter 6 and Chapter 7 are added together into a single dorsal armour count of transverse rows that starts at the posterior edge of the obligate nuchals, and then proceeds along the body and onto the tail until the most posterior of the double-crested caudals is counted. This new variable includes several independent variables within it, but the permit-free scale-count has the significant advantage that the data can be taken through a telescope, or from appropriate photographs, without the researcher's having to catch and to handle the crocodile. A tourist's snap-shots or camcorder photos of an animal on exhibit at a zoo, if properly inclusive and taken from a reasonable angle, satisfies the requirements for this special *Osteolaemus* technique, and thus this new kind of count has the potential to significantly increase sample size in future studies of African dwarf-crocodile scalation variation.

Adding the anterior-end variable's result data to the posterior-end variable's result data was not in Ross + Mayer (1983), but as an experiment the sum of the two characters is here (starting below in Table 8.1) analysed as a single and unified character to test its utility in African dwarf-crocodiles, for the purpose of supporting the recognition of *Osteolaemus tetraspis osborni* (Schmidt) as a regulated C.I.T.E.S. subspecies. This new character is called the "permit-free" scale-count in this study, because no official permit is needed to do it. Thus, if the *Osteolaemus* permit-free scale-count is found to reliably distinguish the two subspecies of African dwarf-crocodiles, then it will have considerable value for C.I.T.E.S. identification of commercial "hornback" (dorsal armour) hides, and stuffed examples, and most importantly for living animals.

Note that the permit-free scalation character, although called a "scale-count" in a general sense, is actually a count of transverse rows of dorsal scales. It has the advantage that, assuming general bilateral symmetry, the long-axis of the animal can be viewed from the side at a dorso-lateral angle, as opposed to the necessity for seeing the entirety of the dorsal scalation from directly above the crocodile. This is a subjective factor, but when an official Endangered Species is involved, getting directly on top of a living example for long enough to count its individual scales, or even just its scale rows, usually requires formal permission.

8.2 METHODS

This special *Osteolaemus* permit-free count is the sum of the two kinds of dorsal scalation characters from Chapter 6 (DCC's) and Chapter 7 (PC's) combined. The result is a single scale-count that starts on the neck at the posterior edge of the obligate nuchal scale-pairs, and then proceeds across the cervico-thoracic juncture and along the length of the body and onto the tail until the most posterior transverse row of the double-crested caudal series is counted (see Figure 8.1 below).

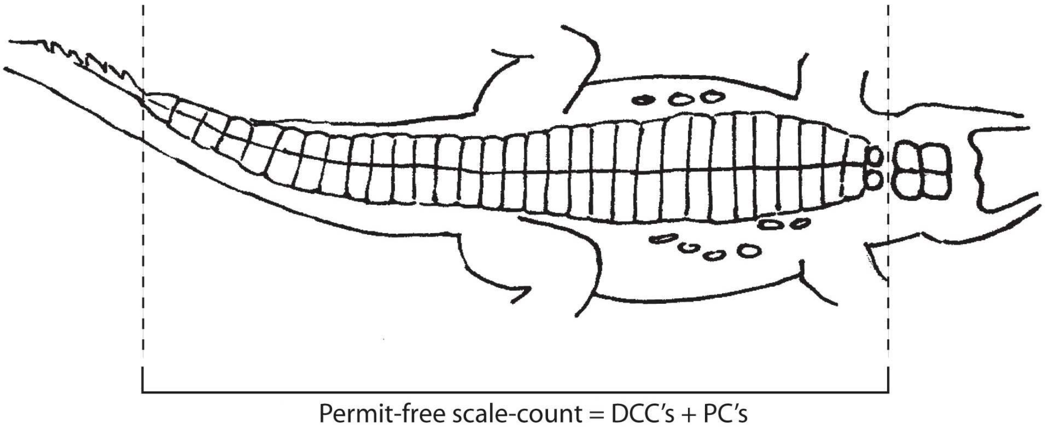


Figure 8.1 Permit-free scale-count on the body
The result of the combined scale-count (= permit-free scale-count) on this male African dwarf-crocodile from Congo-Brazzaville at Likouala (= INTERIOR) is 32 rows (number of DCC's = 13 rows; and number of PC's = 19 rows). The abbreviation DCC means double-crested caudals, and PC means the precaudal transverse rows of dorsal scales, but in this case, the PC's do not include the two transverse rows of obligate nuchals, nor the scattered post-occipital rows anterior to the nuchals.

8.3 RESULTS

The *Osteolaemus* permit-free character data is presented in several tables below. An exploratory distinction is made between low counts, and high counts, of the new sum of two kinds of vertebral-based numbers, starting with “low counts” in Table 8.1, below. Later, after examination of the permit-free scale-count as a single number (low, middle, or high?), the results are further analysed with reference to the Ross + Mayer (1983) component parts of the special *Osteolaemus* permit-free scale-count character.

Table 8.1 Low counts of all rows present in the PC-19 through to C-14 region

PC+DCC=	locality of the cited *Osteolaemus* sample	n=
27 rows	Gabon, at Kango COAST = *O. t. tetraspis*	1
--- --- --- --- ---	one African dwarf-crocodile out of 68 total	
PC+DCC=	locality of the cited *Osteolaemus* sample	n=
28 rows	Gabon, at Gamba COAST = *O. t. tetraspis*	1
28 rows	Cameroon, at Mundemba & Campo Maan COAST	2
--- --- --- --- ---	three African dwarf-crocodiles out of 68 total	
PC+DCC=	locality of the cited *Osteolaemus* sample	n=
29 rows	Gabon, at Setté Cama COAST	1
29 rows	Cameroon, at Yaoundé COAST = *O. t. tetraspis*	3
29 rows	Congo-Brazza, at Dembouanou & Pointe-Noire COAST	2
--- --- --- --- ---	six African dwarf-crocodiles out of 68 total	

All ten African dwarf-crocodiles with low permit-free numbers (27-29 rows) are the same subspecies (*Osteolaemus tetraspis tetraspis* Cope), because they are all from Atlantic coast localities.

The low permit-free numbers (27-29) occur exclusively on the Atlantic coast. It is possible that the low numbers in Table 8.1 (above) can be extended even slightly higher with all examples continuing to be the *Osteolaemus tetraspis tetraspis* Cope subspecies. To investigate this question, all of the higher permit-free numbers are reviewed below, starting with a permit-free count of 30 transverse rows in Table 8.2 (below), and then extended to 31-32 rows, as needed.

Table 8.2 Is 30 also a "low" (= COAST) permit-free number?

PC+DCC=	locality of the cited *Osteolaemus* sample	n=
30 rows	Gabon, at Setté Cama COAST = *O. t. tetraspis*	2
30 rows	Cameroon, at four places COAST = *O. t. tetraspis*	13
30 rows	Congo-Brazza, at Pointe-Noire & Youbi COAST	4

--- --- --- --- --- nineteen African dwarf-crocodiles out of 68 total

All nineteen (19) animals with a permit-free count of thirty (30) rows are from the equatorial Atlantic coast of Africa, and therefore by geography they are *Osteolaemus tetraspis tetraspis* Cope. Three coastal nations, at seven local places, are represented in this table.

Yes, the permit-free count successfully continues to distinguish between the two subspecies when extended to 30 rows (PC+DCC). Twenty-nine (29) out of 29 African dwarf-crocodiles from coastal areas with 27-30 permit-free rows are all *Osteolaemus tetraspis tetraspis* Cope. So, next, is it possible to raise the permit-free count to thirty-one, and still get one subspecies? Table 8.3 (below) has the answer.

Table 8.3 Does 31 also always mean COAST subspecies?

PC+DCC=	locality of the cited *Osteolaemus* sample	n=
31 rows	Benin, at Porto Novo COAST = *O. t. tetraspis*	1
31 rows	Gabon, at Kango & Setté Cama COAST = *O. t. tetraspis*	3
31 rows	Cameroon, at Yaoundé & Campo Maan COAST = *O. t. tetraspis*	11
31 rows	Congo, at Bellelo & Pointe-Noire COAST = *O. t. tetraspis*	5
31 rows	Congo, at Likouala INTERIOR = *O. t. osborni*	3

--- --- --- --- --- twenty-three African dwarf-crocodiles out of 68 total

Twenty (20) animals from Benin, Gabon, Cameroon and Congo-Brazzaville COAST have 31 rows. However, another three (3) animals from Congo-Brazzaville at Likouala INTERIOR also have 31 rows present. So, in this sample two subspecies are represented. Now the answer is no.

With both of the two ecological categories (COAST, INTERIOR) represented, Table 8.3 (above) shows that it is not possible to raise the permit-free count to 31 and still always get *Osteolaemus tetraspis tetraspis* Cope as a subspecies. A small minority of animals with 31 rows (PC+DCC) originated from the interior of Brazzaville-Congo (the Ubangi River drainage), which is the *Osteolaemus tetraspis osborni* (Schmidt) subspecies by geography.

Now, in an attempt to achieve a different single subspecies result at the opposite extreme of variation, meaning this time with INTERIOR = *Osteolaemus tetraspis osborni* (Schmidt), Table 8.4 will examine the two highest permit-free numbers recorded by the Zoer 2006-2007 expedition.

Table 8.4 "High" counts of rows present in PC-19 to C-14

PC+DCC=	locality of the cited *Osteolaemus* sample	n=
32 rows	Cameroon, at Yaoundé COAST = *O. t. tetraspis*	3
32 rows	Congo-Brazzaville, at Likouala INTERIOR = *O. t. osborni*	9
32 rows	Zaïre-DRC, at Kinshasa INTERIOR = *O. t. osborni*	1
--- --- --- --- ---	thirteen African dwarf-crocodiles out of 68 total	
33 rows	Cameroon, at Limbe COAST = *O. t. tetraspis*	1
33 rows	Congo-Brazzaville, at Likouala INTERIOR = *O. t. osborni*	2
--- --- --- --- ---	three African dwarf-crocodiles out of 68 total	

Similar to the mixed COAST-INTERIOR results with 31 rows (Table 8.3 above), there is again no success in achieving a single subspecies with 32 rows because the two C.I.T.E.S. ecological (= geographic) zones are represented in this table. The nation of Cameroon is represented at one coastal locality (Yaoundé, n=3), and in contrast ten other animals are from two distinctly INTERIOR localities. The same is true for 33 rows, the highest permit-free count in this sample, where both subspecies are almost equally represented.

This new permit-free count works part of the time, but not always. However, it does not require locating the sacro-caudal juncture (SC-J) that Chapter 5 (above) explained can be found in four ways. Rather, the new sum of two kinds of vertebral-based numbers is a scalation character that has visual limits at its anterior and posterior ends. Transverse rows of contiguous dorsal scales, as defined in Ross + Mayer (1983:305-306), with the notable addition of the nineteenth precaudal row (PC-19) at the base of the neck as an optional extra-thoracic row (an *Osteolaemus* specialty, due to newly discovered "fold" details that complicate the 1983 definition), are combined and thus simplified in the permit-free counting technique for *Osteolaemus* subspecies detection.

The new character identifies all *Osteolaemus* with 27 to 30 of the permit-free rows as *O. tetraspis tetraspis* Cope (Tables 8.1 and 8.2). However, Tables 8.3 and 8.4 show that both subspecies can have higher permit-free counts in the 31, and 32, and 33 range. In the total 2006-2007 sample of African dwarf-crocodiles, 29 out of 68 examples were identifiable to subspecies by permit-free counts, and they were all COAST = *Osteolaemus tetraspis tetraspis* Cope.

It is possible to subdivide the permit-free count at the sacro-caudal juncture (SC-J), which can be located by four different methods in the genus *Osteolaemus* Cope (see Chapter 5, above). Thus the permit-free count becomes several additional characters, because now the variables at the opposite ends of the permit-free series can be separated into independent variables that can be compared with each other, and converted into ratios and proportions of the whole, as discussed (explored) below in Subsection 8.3.1 utilizing Ross + Mayer (1983) in a new and potentially interesting way. This is especially important because the back-edge of the hind-legs method for finding the SC-J works 100% of the time in *Osteolaemus* Cope in the Zoer 2006-2007 expedition sample (n=68), as earlier detailed above in Chapter 5.

8.3.1 The permit-free count subdivided at the sacro-caudal juncture

Calculating the percentage of the total permit-free count that is either precaudal rows (PC's), or alternatively double-crested caudals (DCC's), involves counting both sets of dorsal scales, and the two percentages of results (% of PC's, correlated with % of DCC's) are then compared with each other. In other words, when the PC's is 60,00%, then the DCC's will be 40,00%, because the total is always 100.00% of the permit-free scale-count. In theory the 60% to 40% ratio (just an example) between PC's and DCC's could be achieved in more than one way, but that remains to be tested in Table 8.5 (below) which examines the low range of percentages of the total that are PC rows located anterior to the sacro-caudal juncture (SC-J). In other words, this is the crocodile body, exclusive of the obligate neck, and exclusive of all of the tail. Note thought that although the two transverse rows of obligate nuchals are excluded from this count, the posteriormost possible row of neck-scales (PC-19) is included as a precaudal row that qualifies in the data in Table 8.5 (below).

Table 8.5 Lowest results of PC rows as a percentage of permit-free count

Percentage	locality of *Osteolaemus*	n=	PC's / DCC's
56,67 %	Cameroon COAST = *O. t. tetraspis*	2	17 / 13
--- --- ---	--- --- --- --- --- --- --- --- ---	--- --- ---	--- --- ---
57,14 %	Cameroon COAST = *O. t. tetraspis*	1	16 / 12
57,14 %	Gabon COAST = *O. t. tetraspis*	1	16 / 12
--- --- ---	--- --- --- --- --- --- --- --- ---	--- --- ---	--- --- ---
57,58 %	Cameroon COAST = *O. t. tetraspis*	1	19 / 14
57,58 %	Congo-Brazzaville INTERIOR = *O.t.o.*	2	19 / 14
--- --- ---	--- --- --- --- --- --- --- --- ---	--- --- ---	--- --- ---
58,06 %	Cameroon COAST = *O. t. tetraspis*	3	18 / 13
58,06 %	Congo-Brazzaville INTERIOR = *O.t.o.*	1	18 / 13
--- --- ---	--- --- --- --- --- --- --- --- ---	--- --- ---	--- --- ---
58,62 %	Cameroon COAST = *O. t. tetraspis*	1	17 / 12
58,62 %	Congo-Brazzaville COAST = *O.t.t.*	2	17 / 12
--- --- ---	--- --- --- --- --- --- --- --- ---	--- --- ---	--- --- ---
Percentage	locality of *Osteolaemus*	n=	PC's / DCC's
59,26 %	Gabon COAST = *O. t. tetraspis*	1	16 / 11
--- --- ---	--- --- --- --- --- --- --- --- ---	--- --- ---	--- --- ---
59,38 %	Cameroon COAST = *O. t. tetraspis*	3	19 / 13
59,38 %	Zaïre-DRC INTERIOR = *O. t. osborni*	1	19 / 13
59,38 %	Congo-Brazza INTERIOR = *O. t. osborni*	9	19 / 13

This table shows 28 African dwarf-crocodiles with low percentages of PC's. Two subspecies are represented, and numerous kinds of combinations of PC's and DCC's can occur in both coastal and inland localities, essentially randomly.

The results in Table 8.5 (above) are mixed, and are not conclusive. Therefore an additional and similar examination of higher percentages is necessary, starting with African dwarf-crocodiles on which the correlation is exactly 60,00 % (PC's) and 40,00 % (DCC's), is presented in Table 8.6 (below).

Table 8.6 Precaudal is 60% of permit-free scale-count total

Locality of *Osteolaemus*	n=	PC's / DCC's
Cameroon, at Yaoundé COAST = *O. t. tetraspis*	3	18 / 12
Cameroon, at Mundemba COAST = *O. t. tetraspis*	1	18 / 12
Gabon, at Setté Cama COAST = *O. t. tetraspis*	2	18 / 12
Congo-B at Pointe-Noire COAST = *O. t. tetraspis*	1	18 / 12

Seven (7) animals have a combination of eighteen (18) PC's and twelve (12) DCC's. The 60% PC and 40% DCC combination occurs only on the coast in this sample. The 12 DCC's condition was predicted by Ross + Mayer (1983:328) as the most common number of double-crested caudals (DCC) in *Osteolaemus tetraspis* Cope as a species.

Because of the prediction in Ross + Mayer (1983:328) about the common occurrence of 60% PC's and 40% DCC's the several slightly larger (60,71% and 61,29% etc.) yet "low" examples were not included in Table 8.6 (above), and are now listed in Table 8.7 (below).

Table 8.7 Slightly more than 60% of permit-free scale-count

Percentage=	locality of *Osteolaemus*	n=	PC's / DCC's
60,71 %	Cameroon, at Mundemba COAST	1	17 / 11
61,29 %	Benin, at Porto Novo COAST	1	19 / 12
61,29 %	Cameroon, at Yaoundé COAST	4	19 / 12
61,29 %	Cameroon, at Campo Maan COAST	4	19 / 12
61,29 %	Gabon, at Setté Cama COAST	2	19 / 12
61,29 %	Gabon, at Kango COAST	1	19 / 12
61,29 %	Congo-Brazzaville, at Bellelo COAST	4	19 / 12
61,29 %	Congo-B, at Pointe-Noire COAST	1	19 / 12
61,29 %	Congo-B, at Likouala INTERIOR	2	19 / 12

Twenty (20) African dwarf-crocodiles from the Zoer 2006-2007 expedition sample in which the PC's are slightly more than 60% of the permit-free scale-count total. Both subspecies are represented in this table.

Although the percentage is slightly more than 60% in Table 8.7 above, most of the specimens are from coastal localities similar to the animals that were earlier listed in Table 8.6 above (60% PC's and 40% DCC's). The African dwarf-crocodiles on which the precaudals are more than 62% of the permit-free scale-count total are displayed lastly, in Table 8.8 below.

Table 8.8 PC's more than 62% of permit-free scale-count total

Percentage=	locality of *Osteolaemus*	n=	PC's / DCC's
62,07 %	Cameroon, at Yaoundé COAST	2	18 / 11
62,07 %	Gabon, at Setté Cama COAST	1	18 / 11
--- --- --- ---	--- --- --- --- --- --- --- --- ---	--- ---	--- --- ---
63,33 %	Cameroon, at Yaoundé COAST	2	19 / 11
63,33 %	Cameroon, at Mundemba COAST	1	19 / 11
63,33 %	Cameroon, at Campo Maan COAST	3	19 / 11
63,33 %	Cameroon, at Limbe COAST	1	19 / 11
63,33 %	Congo-B, at Youbi COAST	1	19 / 11
63,33 %	Congo-B, at Pointe-Noire COAST	2	19 / 11

The highest results of precaudal percentage of permit-free scale count, being 62,07% and 63,33%, are listed in this table. All thirteen (13) animals above are COAST and thus are the subspecies *Osteolaemus tetraspis tetraspis* Cope, according to the C.I.T.E.S. geographic definition.

The *Osteolaemus* permit-free count of transverse rows of dorsal armour is diagnostic for *Osteolaemus t. tetraspis* (the COAST localities) when the number of permit-free scale rows is small (27-30). Similarly, but not logically following from the above, the percentage of the permit-free count that is PC rows is diagnostic for *O. t. tetraspis* when it is large (62,07% - 63,3%). This apparent contradiction suggests that individual variation is significant, and further that subdividing the *Osteolaemus* permit-free count into precaudal and caudal parts does not significantly improve certainty.

In the next chapter (Conclusion) a review of all of the characters that were individually discussed in Chapter 2 through Chapter 8 (this chapter) will answer the question: "What African dwarf-crocodile scale-counts best support C.I.T.E.S. recognition of *Osteolaemus tetraspis osborni* (K.P. Schmidt)?" when the African dwarf-crocodile species (*Osteolaemus tetraspis* Cope) is subdivided into subspecies defined as the COAST and INTERIOR geographic categories.

8.4 REVIEWING THE NEW PERMIT-FREE DORSAL SCALATION CHARACTER

The two component parts of the *Osteolaemus* special permit-free scale-count are each an independent variable. The anterior end of this new combined character can be any of several transverse rows of dorsal scales, and the same is true about the posterior end of the series of rows that gets counted. In some cases, the new permit-free scale-count character has advantages. In this thesis the adding together of two formerly independent kinds of dorsal armor variation was an experiment, and it has produced an unexpected result. Neither of the two subsets within the permit-free count are totally diagnostic to subspecies in this sample of African dwarf-crocodile (n=68), but the permit-free count is actually not any more unreliable (not predictive 100% of the times) than either of its component parts. Rather, the predictive value of this new character appears to be actually as good as, or possibly even better than, the double-crested caudals (DCC's) alone, or the continuous precaudal (PC's) alone, even when the Ross + Mayer (1983) definition is modified to include PC-19 in *Osteolaemus tetraspis* Cope. Now, with PC-19 defined as part of the continuous precaudal armor, this new method takes less time to count. It is quicker to count the whole series, than it is to locate the sacro-caudal juncture (SC-J) and then count the PC's and DCC's separately. The advantage for field-work is that the two transverse rows of obligate nuchals are anterior to, and are excluded from, the permit-free count, and similarly all of the single-crested caudals are posterior to, and are excluded from the permit-free count. Both ends of this new dorsal-scalation character are reasonably obvious, and in *Osteolaemus tetraspis* can often be seen through a telescope or in a photograph of the animal, when its body is not covered by water. It is not always necessary to capture and handle the reptile for detailed examination, nor is it necessary to view the African dwarf-crocodile form directly above it. Rather, this special *Osteolaemus* permit-free count can often be made when the animal is seen in dorso-lateral view, which is common in wildlife and zoo situations.

CHAPTER IX CONCLUSION: SOME SCALATION CHARACTERS ARE INTERESTING, BUT NONE WORK PERFECTLY

(in *Osteolaemus tetraspis* Cope, 1861, the African dwarf-crocodile, a C.I.T.E.S. Appendix I crocodilian)

9.1 A PROCESS OF EVALUATION THAT LEADS TO AN ANSWER

From the already existing published literature, it had appeared to be possible that one or more of the general kinds of scalation characters discussed in Chapters 2-8 could convincingly identify and separate African dwarf-crocodiles into the two C.I.T.E.S. subspecies for 100% of the individual *Osteolaemus tetraspis* that were examined by the 2006-2007 expedition. However, the new data now presented in this thesis has shown that the traditional crocodilian scalation characters (the post-occipitals, the nuchals, the two kinds of ventral scale counts, the double-crested caudals, and the precaudal transverse rows between the tail and the neck) each fails on its own to identify 100% of the animals in the total sample (n=68 *Osteolaemus* with locality data) from the 2006-2007 expedition.

Different dorsal and ventral scalation characters fail to be 100% predictive to subspecies in *Osteolaemus* (defined the C.I.T.E.S. geographic way as a list mostly of nations) for various reasons, often involving overlap between COAST results and INTERIOR results. All of the dorsal and ventral scale-count characters discussed in Chapters 2-8 have produced results that include some animals for which no C.I.T.E.S. defined subspecies is exclusively indicated. However, the results from some of the characters appear to predict one or the other subspecies at least some of the time. For example, although there was overlap in Chapter 6 between COAST and INTERIOR results about the number of transverse rows of double-crested caudal scales (DCC's), there were some outcomes that occurred only in one subspecies. Thus, in this case, if an individual *Osteolaemus* has an extremely low DCC count, then the animal can be identified to subspecies. The same is true about specimens with extremely high DCC results, but significantly unfortunately there are many African dwarf-crocodiles that have neither extremely low DCC's, nor high DCC row counts, and all of these results in the middle are not diagnostic to subspecies.

In this concluding chapter, the various scalation characters will each be evaluated for their amount of predictiveness in the choice between the two C.I.T.E.S. defined (COAST and INTERIOR) subspecies categories (Section 9.2), followed by a general conclusion and final recommendation in Section 9.3.

In the end, an answer will be given to the question about what individual kind of scalation character best supports the C.I.T.E.S. hypothesis. In theory, even if none of them are perfect (100% predictive as a character kind), it should be possible to make a prediction about the subspecies identification of a limited percentage of any sample of these animals. However, it is generally beyond the scope of this thesis to ask questions about exactly which kinds, and about how many characters would be required to work in combination to achieve a diagnostic to subspecies result. It takes a lot of work to accurately report any one of these characters, and this chapter searches for the single most productive scale-counting activity. If other researchers wish to do statistics on suites of separate kinds of scalation characters, the data is available. Note that exceptions to the generality about “single characters” include the two kinds of ventral counts combined, and also the combination of three characters that produced the permit-free method. It is possible that one kind of character, or an exceptional combination of two or more related characters, will be substantially better than all of the others. An additional consideration in the evaluation of the utility of these choices between alternative kinds of scalation characters is the physical and technical difficulty involved in the character itself. Some few are relatively simple and reliable, but many are remarkably difficult to apply, often involving specialist training and the application of extremely precise definitions. Similarly, the vast majority of scalation characters, especially the pair of ventral counts, require physically handling the animal, and thus the level of difficulty is greater, especially in the case of a C.I.T.E.S. Appendix 1 animal, because official permission to closely and physically examine and record scientific scalation data on crocodilians in the wild (and many other situations) in Africa is usually required.

9.2 INDIVIDUAL CHARACTERS EVALUATED FOR SUBSPECIES IDENTIFICATION VALUE

9.2.1 The C.I.T.E.S. hypothesis about two subspecies in *Osteolaemus tetraspis* Cope

The original Schmidt (1919) act of creating a second taxonomic kind of African dwarf-crocodile(s) was based primarily on the internal anatomy of the animal’s nose. Thus, the taxon *Osteoblepharon osborni* Schmidt, 1919, was originally differentiated from the older taxon *Osteolaemus tetraspis* Cope, 1861, by a cranial character that can only be examined on cleaned and carefully prepared skulls. All of the scalation characters that the literature has suggested might distinguish the modern subspecies *Osteolaemus tetraspis tetraspis* Cope from the subspecies *Osteolaemus tetraspis osborni* (Schmidt) have been secondary attempts to find any diagnostic character that is externally visible.

Assuming that the degree of ossification of the otherwise cartilaginous septum (divider) between the two external nostrils (the individual nose holes) is a diagnostic character (completely bony, or alternatively incompletely bony) for separating these two subspecies, the nasal septum is internal (under the skin), and requires dissection (or possibly x-ray). Thus, C.I.T.E.S. desperately needs an externally visible character that can be seen on living animals.

9.2.2 The post-occipital scales in Chapter 2 evaluated as a predictor of these two C.I.T.E.S. subspecies

The assertion that today's two C.I.T.E.S. taxa of African dwarf-crocodiles (*Osteolaemus tetraspis tetraspis* and *Osteolaemus tetraspis osborni*) can be identified to subspecies by the number and placement of the post-occipital scales (PO's) originated in Schmidt (1919), but the hypothesis was tested by Inger (1948), and was found to lack merit as a truly predictive character in African dwarf-crocodiles. In hindsight, it appears that the literature indicated that the number of specimens in the sample of *Osteolaemus tetraspis* can influence results, because the Inger (1948) sample was more numerous than the Schmidt (1919) sample of this dwarf-crocodile species.

Displayed simply as the C.I.T.E.S. defined COAST and INTERIOR dichotomy between *Osteolaemus tetraspis tetraspis* Cope, 1861, and *O. t. osborni* (K.P. Schmidt, 1919), the most relevant results from Chapter 2 are summarized in Table 9.1 (below), where horizontal lines A-D are 2-row kinds (four choices of arrangement), and lines E-F are 1-row kinds (with three arrangement choices).

Table 9.1 Comparing the two-subspecies hypothesis with the new data about the post-occipital scales (n=57)

	O. t. tetraspis	*O. t. osborni*
A) Two transverse rows of four each	3 out of 42	3 out of 15
B) Four in anterior row, two in posterior row	9 out of 42	9 out of 15
C) Two in anterior row, four in posterior row	3 out of 42	1 out of 15
D) Other arrangements in two rows	3 out of 42	1 out of 15
--- --- --- --- --- --- --- --- --- ---	--- --- --- --- ---	--- --- ---
E) Four scales in single transverse row	20 out of 42	1 out of 15
F) Two scales present in the only row	2 out of 42	0 out of 15
G) Other kinds of single-row PO's	2 out of 42	0 out of 15

This table presents the arrangements of post-occipital scales (PO's) in the two supposed subspecies. Although the placement of PO's in just one row (lines E-G) occurs remarkably often (24 out of 42) in *O. t. tetraspis* in this sample, a significant number (18 out of 42) of African dwarf-crocodiles from the Atlantic coast (being the COAST taxon, *O. t. tetraspis*) have their PO's arranged in two transverse rows (lines A-D). Similarly, some (1 out of 15) *O. t. osborni* from the continental INTERIOR have one row of PO's (lines E-G), but others (14 out of 15) have two rows of post-occipital scales (lines A-D). An animal with only one row could be either subspecies, and the same is true about dwarf-crocodiles with two PO rows. Therefore, the post-occipitals are not a 100% reliable character for the recognition of *Osteolaemus tetraspis osborni*, K. P. Schmidt.

The final assessment of the predictive value of the post-occipital scales (when interpreted the C.I.T.E.S. way as one or two transverse rows) is presented, in separate graphs (one for each taxon) as the percentage of confidence for subspecies taxonomic identification within each of the two subspecies categories, in Figure 9.1 (below).

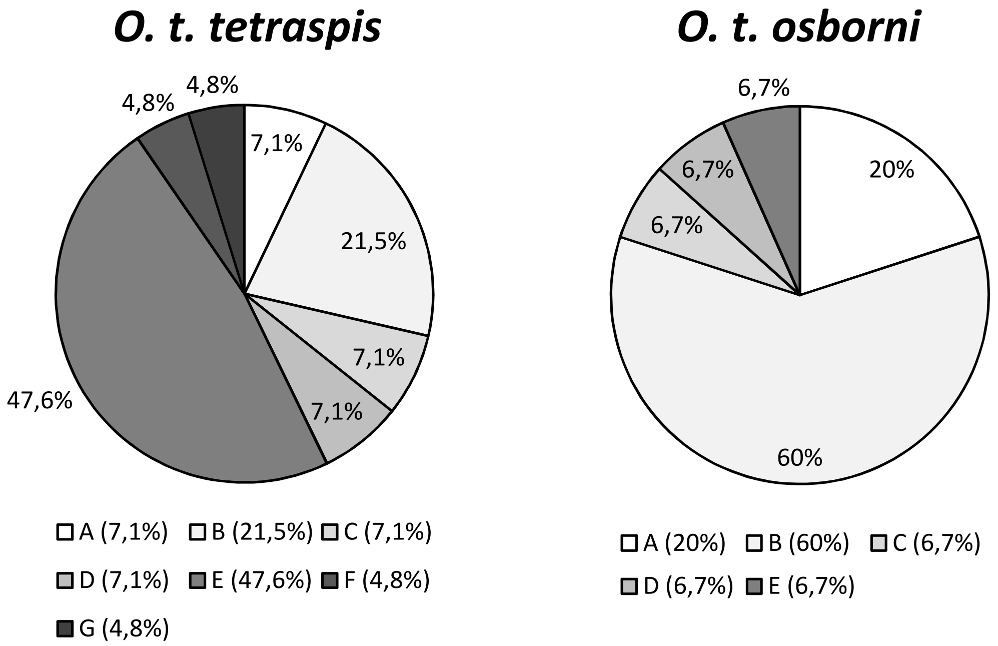


Figure 9.1 Post-occipital scales in two taxa of African dwarf-crocodiles

The category letters (A-G) in the legend of this figure correspond with the same letters (A-G) located to the left-side of the seven different arrangements of PO's listed in Table 9.1 (above). The white and lighter gray tones (A-D) represent animals with their PO's in two transverse rows, while in contrast the darker gray tones (E-G) represent African dwarf crocodiles in groups with single-row PO's.

Variation in the post-occipital (PO) scales was originally thought by K.P. Schmidt (1919) to be a diagnostic identification character for separating the COAST and INTERIOR taxa from each other. Note that the genus *Osteoblepharon* Schmidt, 1919, had the type species *Osteoblepharon osborni* Schmidt, 1919, and the new genus was based on the nasal septum (incompletely ossified in *Osteoblepharon* Schmidt, but in contrast completely ossified in *Osteolaemus* Cope). However, it was actually in the type description of the species *Osteoblepharon osborni* Schmidt that the post-occipital scalation difference between *Osteoblepharon osborni* and the species *Osteolaemus tetraspis* was mentioned by Schmidt (1919:424). Either way, as separate genera or separate species, or further as separate subspecies (COAST and INTERIOR) of one species, the PO hypothesis in Schmidt (1919) is not supported by the new (n=57) data.

9.2.3 The nuchal scales in Chapter 3 evaluated as a predictor of these two C.I.T.E.S. subspecies

The literature contains no (zero) assertions that any of the different kinds of variation among and involving the nuchal scales (the nuchals) are diagnostic for the subspecies *Osteolaemus tetraspis tetraspis* compared with *Osteolaemus tetraspis osborni*. However, because the data was available, this thesis examined the nuchals in greater detail than most earlier studies, and with a large number of specimens. The 2006-2007 expedition's results included the unexpected presence of fusions (the joining, by co-ossification, of two bones into one), and also midline irregularities between pairs of individual nuchal scales, but these fusions and also these cases of bilateral asymmetry are rare. These special and unusual phenomena are expected to occur in both *O. t. tetraspis* and *O. t. osborni* when larger samples are defined as COAST and INTERIOR taxa with the traditional C.I.T.E.S. distributions.

Displayed as COAST (*O. t. tetraspis*) and INTERIOR (*O. t. osborni*) subspecies taxa, the most relevant results from Chapter 3 are summarized in Table 9.2 (below).

Table 9.2 The theoretical hypothesis that the nuchals could identify subspecies, compared with the new data (n=61)

	O. t. tetraspis	*O. t. osborni*
Anterior row longer than middle row	41 out of 47	14 out of 14
Anterior row equal to middle row	2 out of 47	0 out of 14
Anterior row shorter than middle row	4 out of 47	0 out of 14
--- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- --- ---		
Transverse fusion of nuchals	0 out of 53	2 out of 15
Lengthwise fusion of nuchals	1 out of 53	0 out of 15
PC-19 is present	31 out of 53	14 out of 15

This table shows the most relevant results on the length comparison of the two obligate rows of nuchals, the fusion of nuchals (both transverse and lengthwise), and the presence of PC-19 (being the optional posteriormost row of nuchals). Note that transverse and lengthwise fusions among the obligate nuchals are uncommon enough that they are excluded from consideration as a subspecies indicator, because of the small number of crocodiles in the relevant samples. Not included in this table are midline zig-zag irregularities, which occur more frequently in *O. t. tetraspis* (larger sample size) but rarely. Aberrations such as fusions and zig-zags can occur in both taxa, and similarly the presence of PC-19 can be found some of the time in both COAST and INTERIOR categories.

The general literature prediction, exemplified by Ross + Mayer (1983), was that the two transverse rows of obligate nuchals are always composed of scales that are physically larger than the scales (when present) in the optional posteriormost row of the three in *Osteolaemus tetraspis* Cope. This was true in 100% of the new (n=61) sample. However, Ross + Mayer (1983:319) explicitly observed that the anteriormost of the two large transverse pairs of nuchals is usually longer longitudinally (along the long-axis of the animal) than the pair of obligate nuchals immediately posterior to it. This hypothesis is diagrammatically explored in Figure 9.2 (below).

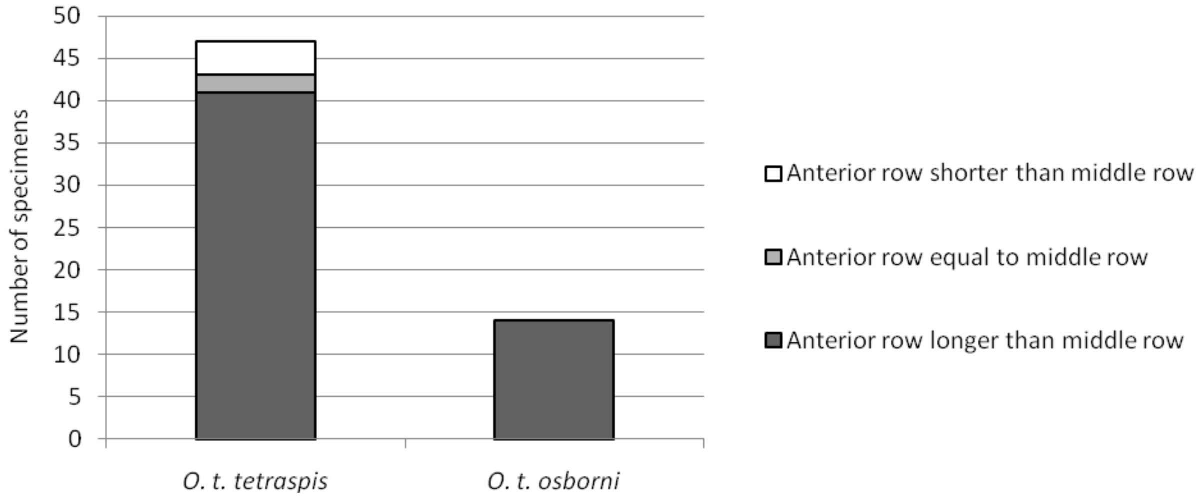


Figure 9.2 Length comparison of the big obligate nuchal scales

This diagram presents the results of the comparison in length between the two big obligate neck scale rows. These are the anterior row and the middle row of nuchals. In both subspecies the anterior obligate row is the longer of the two in the vast majority (55 out of 61) of these African dwarf-crocodiles. Note that only six animals in this sample (n=61) show a different pattern.

Although the anterior row is only shorter or equal in length in the COAST taxon *O. t. tetraspis*, the overwhelming majority of dwarf-crocodiles in this subspecies have their anterior row longer than the middle row of nuchals. The 100% result in the INTERIOR (*O. t. osborni*) sample could easily be influenced by the small number of specimens in that geographic group. There is considerable taxonomic overlap in the result that the anterior row is longitudinally longer (the tested hypothesis), and therefore the nuchals are not a 100% reliable character for distinguishing the two C.I.T.E.S. subspecies in *Osteolaemus tetraspis* Cope from each other.

9.2.4 The two kinds of ventral scale-counts in Chapter 4 evaluated as predictors of these two C.I.T.E.S. subspecies

The literature had predicted overlapping ranges of variation in both of the two kinds of ventral scalation characters when the subspecies *Osteolaemus tetraspis tetraspis* Cope is compared with the subspecies *Osteolaemus tetraspis osborni* (Schmidt). However, some few cases of extremes of variation were formerly thought to have predictive value for identification to subspecies. The collar-vent (C-V) count, and the number of ventral scales across the widest level of the belly, are of special importance to C.I.T.E.S. because they are external scalation characters that are available on commercial belly hides as raw skins, and also as finished leather.

Displayed as COAST (*O. t. tetraspis*) and INTERIOR (*O. t. osborni*) subspecies taxa, the most relevant results from Chapter 4 are summarized as two independent kinds of counts (below). Both of these two ventral scalation characters require detailed examination (or appropriate photos) of the belly-skin surface of the animal, and thus they share the potential of a considerable difficulty being encountered about gaining permission to turn a living or dead African dwarf-crocodile onto its back for scientific purposes.

Table 9.3 Comparing the two-subspecies hypothesis with the new data about two counts on the belly (n=47)

	O. t. tetraspis range	*O. t. osborni* range
The collar-vent (C-V) count	22 to 28 rows	21 to 23 rows
The transverse scale-count	8 to 14 scales	11 to 12 scales

This table presents the two ventral characters from Chapter 4. Note that because the “midline” (a term with two alternative definitions) longitudinal count of transverse rows is independent from the count of the number of ventral scales across the widest level of the belly, these two C.I.T.E.S. characters are examined in two separate graphs (below). Also note that the number of COAST animals is relatively large, especially when the INTERIOR sample for these ventral counts is extraordinarily small. This discrepancy was caused by factors beyond the control of the expedition. In this case, a major part of the sample required permission to turn the animals onto their backs for examination purposes, and permission was denied.

The overlap in the new results about only the C-V (collar-vent) count is visually presented as a diagram in Figure 9.3 (below). The C-V numbers are the range of variation in the number of rows (between two defined limits) crossing the ventral midline. In contrast, the transverse count is the range of variation in the number of individual “ventral scales” (a defined term) across the animal’s belly. The C-V counts of both taxa overlap each other when 22 or 23 rows are present, and similarly (but graphed separately) the two C.I.T.E.S. taxa can both have 11 or 12 ventral scales in their mid-belly transverse row.

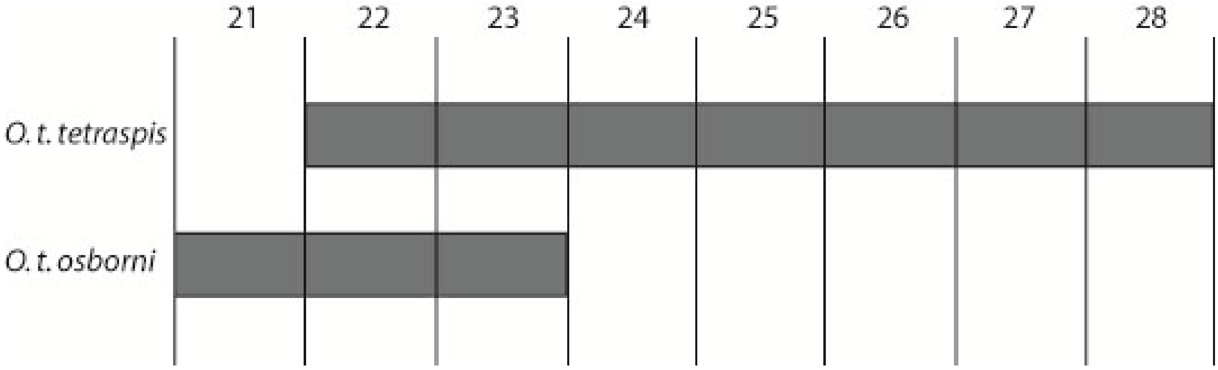


Figure 9.3 Collar-vent count in two taxa of African dwarf-crocodiles

Apart from the part of the ranges of the C-V count in these subspecies that do overlap (22+23 rows), the outcomes that do not overlap each other are both low counts (21 rows) and high counts (24-28 rows). However, there is the subjective factor that the *O. t. osborni* results plotted in this horizontal bar-graph are from a relatively small INTERIOR sample.

The overlap in the new (n=47) results about just the transverse count of ventral scales across the widest part of the crocodile's belly is similarly diagrammatically presented in Figure 9.4 (below).

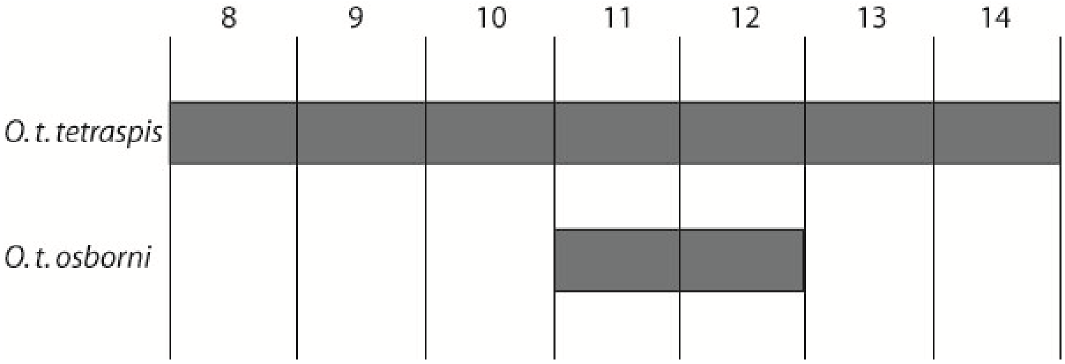


Figure 9.4 Transverse scale-count results from the bellies of both taxa compared

The ranges of the transverse scale-count on the belly also overlap (11-12 scales), and they notably also have both low (8-10 scales) and high (13-14 scales) outcomes as non-overlapping results. The overlap is in the middle, and therefore it can be hard to distinguish one subspecies from the other utilizing this scale-count character, based on the limited data from the 2006-2007 sample.

The two basic kinds of ventral characters in Chapter 4 are different from the scale counts in other chapters in more than one way. It is important that these two are the only counts made on the belly, but in addition to that the two kinds of ventral counts are both based on two or more individual counts. The King + Brazaitis (1971) method involves making two parallel C-V counts (each of which has a result), and although the classical second character is the number of ventral scales in the widest transverse row (singular), the Zoer 2006-2007 expedition recorded the number of ventral scales in the three widest rows (each of which has a result). Therefore, the overlap that occurs between the two subspecies in this sample needs supplementary explanation, as detailed in Table 9.4 (below).

Table 9.4 Number of animals without any overlap in their two kinds of belly count results (n=47 for each method)

	O. t. tetraspis	*O. t. osborni*
No overlap with other subspecies in C-V count	27 out of 44	0 out of 3
No overlap in the transverse scale-count	5 out of 44	0 out of 3

Table 9.4 shows the number of animals that have no overlapping results in the C-V count and the transverse scale-count on the belly. The two ventral scale-counts (the collar-vent count and the transverse scale-count) both contain more than one result for each count in an individual animal. The C-V (collar-vent) count consisted of two parallel counts on the belly (to the left and to the right of the midline). Only if both of these results are not overlapping with

the outcomes of the other subspecies, then this individual is counted (27 out of 44) in *O. t. tetraspis*. The same is true about the transverse scale-count, in which the number of scales was counted in the three broadest belly rows (the 8th, 9th, and the 10th rows from the gular collar). Thus, only when all three individual outcomes do not overlap with the results of the other subspecies are they counted. For example, the result 0 out of 3 INTERIOR animals means zero out of three, even when counted three ways (rows 8-10). In a sense it is 0 out actually 9 transverse rows (3x3) across a defined zone of belly skin.

Note that expedition data about the C-V (collar-vent) count will also be compared with the various existing published hypotheses about this ventral scalation character (below) later and separately in this chapter (Tables 9.9 and 9.10). Similarly, the relevant hypotheses from the literature about the C.I.T.E.S. transverse count of midbelly ventral scales will also be tested with the new data (n=47) in both Table 9.9 and Table 9.10 (below).

9.2.5 The back-edge of the hind legs in relation to the SC-J as a predictor of these two C.I.T.E.S. subspecies

In Chapter 5 it was a surprise that the Ross + Mayer (1983) dividing line between the body and the tail on all of the new *Osteolaemus* specimens coincided with the level of the back-edge of the skin and muscle covered femur part of the hind legs (criterion #4, the traditional method). However, because this phenomenon occurred in 100% of the samples of both *O. tetraspis* subspecies, the result is not of any taxonomic utility. Similarly, the expedition's results about which caudal row of scales is the first to ventrally pass posterior to the cloacal oval were variable and overlapping, and failed to reliably discriminate between the two C.I.T.E.S. subspecies as COAST (*O. t. tetraspis*) and INTERIOR (*O. t. osborni*) categories.

Displayed as COAST and INTERIOR subspecies taxa, the three new (as opposed to the additional traditional option) Ross + Mayer (1983) method kinds of results from Chapter 5 are summarized as a group in Table 9.5 (below).

Table 9.5 Disagreement among methods of finding PC-1 and the SC-J could possibly help identify subspecies when n=68

	O. t. tetraspis	*O. t. osborni*
Criterion 1 (feeling the iliac crest)	53 out of 53	15 out of 15
Criterion 2 (outstretched femurs)	36 out of 36	13 out of 13
Criterion 3 (width of PC-1)	52 out of 53	15 out of 15

The two skeleton-based methods (criteria 1 + 2) overwhelmingly confirm each other, and the third method works almost all of the time. Criteria 1 + 2 were the method of finding PC-1 and the SC-J for the further purpose of testing criterion 3 (and also for testing the traditional criterion 4). Note that criterion 3 has a 98,5% rate of success, because in one animal the width did not confirm the pelvis and the femur bones methods. The results from this table about the three Ross + Mayer (1983) methods will be presented as vertical column-diagrams in Figure 9.5 (below).

The Ross + Mayer (1983) hypothesis for all living taxa of crocodilians was that criterion 1 and criterion 2 should always essentially agree with each other, but criterion 3 is slightly less reliable and it can sometimes disagree. This predicted result is definitely true in the *Osteolaemus tetraspis* species in this sample of 68 animals. In theory it could be predicted that if any discrepancies about criterion 3 are found, they should be rare, and thus the larger the sample, the better chance of recording this phenomenon. This is also shown to be true in Figure 9.5 where this sample-size factor, and also the two C.I.T.E.S. subspecies, are graphically (vertical column diagrams) compared with each other.

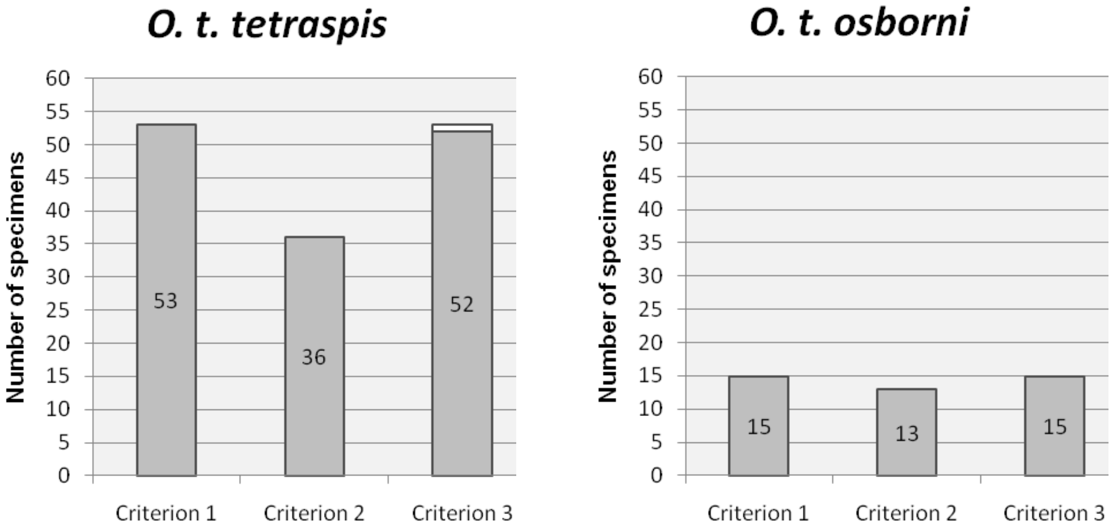


Figure 9.5 Finding PC-1 and the SC-J in two taxa of African dwarf-crocodiles

All three of the Ross + Mayer (1983) methods of finding PC-1 and the SC-J are essentially equally successful in both subspecies. The width of PC-1 failed to confirm pelvis and femurs in only one animal out of 53. Therefore, the comparative results of these three methods are not useful as an identification character in this subspecies dichotomy.

Note that there were four methods discussed in Chapter 4, but the results about criterion #4 (the level of the back-edges of the outstretched hind limbs) are 100% in agreement with criteria #1 and #2. Therefore, criterion 4 is not tabled or graphed here. However, it is a surprising benefit to science, because the anterior edge of the tail (the SC juncture) is functionally the same transverse level in all reports about the number of transverse dorsal body rows, and also all data about the number of caudal whorls, including the number of transverse rows of tail scales anterior to the start of the single-crested caudals (the knife-edge dorsal swimming keel). In this thesis the number of SCC scales are not reported, but the transverse DCC (double-crested caudal) rows are a major topic.

9.2.6 The double-crested caudals in Chapter 6 evaluated as a predictor of these two C.I.T.E.S. subspecies

Because the sacro-caudal juncture can be reliably located four ways, including using the back-edge of the hind legs method in *Osteolaemus tetraspis*, and because the differentiation of the dorsal transverse tail-whorls into double-crested caudals and single-crested caudals is unambiguous in African dwarf-crocodiles, the DCC data from all of the literature can be confidently compared with the DCC numbers recorded in the 2006-2007 field-sample. The literature included one hypothesis, published by Inger (1948), that DCC numbers would separate *Osteolaemus tetraspis tetraspis* from *Osteolaemus tetraspis osborni* reliably, but that hypothesis will be falsified separately (below), after the data about the new and significantly larger sample (n=68) is presented in total in Table 9.6 (below).

Table 9.6 The new data about the number of transverse rows of double-crested caudals (n=68)

	O. t. tetraspis	*O. t. osborni*
11 DCC's	15 out of 53	0 out of 15
12 DCC's	29 out of 53	2 out of 15
13 DCC's	8 out of 53	11 out of 15
14 DCC's	1 out of 53	2 out of 15
Range	11 to 14	12 to 14

Finding DCC = 13 (8 out of 53) and DCC 14 (1 out of 53) in the COAST subspecies was unexpected, making it harder than previously thought to identify any individual *Osteolaemus tetraspis* animal to subspecies by its number of double-crested caudal rows, unless it has only 11 or 10 of them, which currently appears to be diagnostic for the *O. t. tetraspis* subspecies as defined by C.I.T.E.S. Note that C-10 occurred in neither the Inger (1948) sample, nor in the Zoer sample. Also note that 11 DCC's did not occur in the 15 individual *Osteolaemus tetraspis osborni* specimens examined during the Zoer expedition.

Despite it being true that the result of 11 DCC's (double-crested caudal rows) did not occur in the INTERIOR sample, and further true that the results of 12-14 DCC's are characteristic of the *O. t. osborni* subspecies, the Inger (1948) hypothesis is not supported. Paraphrased and simplified, the 1948 prediction was that 11 DCC's = *tetraspis*, while (in contrast) 12-14 DCC's = *osborni*. However, the part of Inger's hypothesis about 11 DCC rows across the tail does not work in the newer (n = 68) larger sample, because results of 12-14 DCC's occur remarkably frequently (38 out of 53) in the COAST (*Osteolaemus tetraspis tetraspis*) taxon, causing considerable overlap, as the horizontal bar-diagram in Figure 9.6 (below) illustrates.

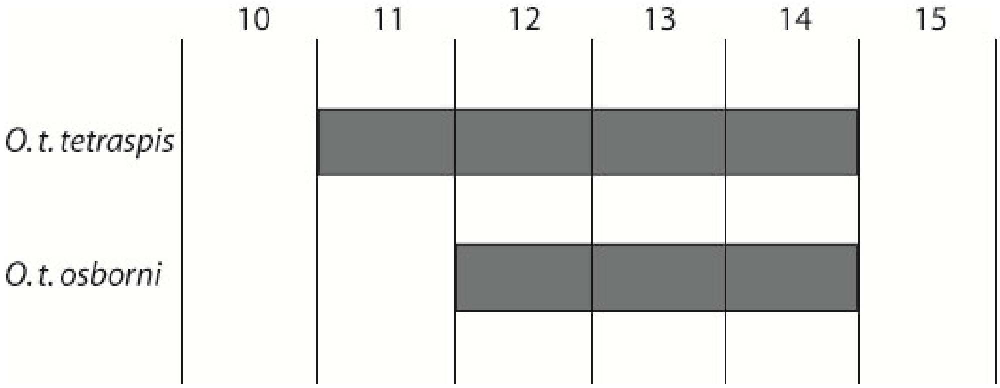


Figure 9.6 DCC counts often overlap between both taxa of *O. tetraspis*

The number of double-crested caudals (DCC's) in the 2006-2007 sample falsified the prediction in Inger (1948) that absolutely no overlap (0,00%) in DCC numbers happens between the subspecies. Note that the Inger and other additional hypotheses from the literature about this count of transverse rows across the tail will be separately compared in detail with the new data (n=68) later, in Tables 9.9 and 9.10 (below). For now, though, it is safe to say that the overlap in this character is broad and general enough that only a relatively small percentage of the African dwarf-crocodiles in this n=68 sample can be identified to subspecies.

When the total (68 animals) is divided into two geographic subspecies, it becomes evident that the larger (more numerous) taxonomic sample (COAST = *tetraspis*) exhibits a slightly greater degree of variation than the smaller (INTERIOR = osborni) sample. The new results about the DCC character are graphed as percentages of each subspecies sample in the pair of pie-diagrams in Figure 9.7 (below).

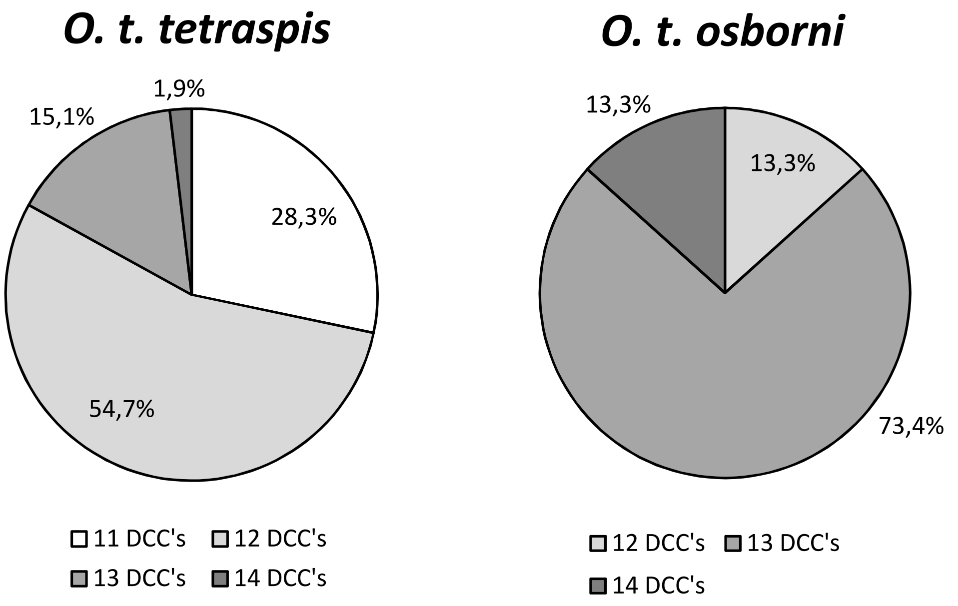


Figure 9.7 Frequency of occurrence of numbers of double-crested caudals in two compared kinds of *Osteolaemus*

This pair of diagrams presents the DCC character's results in percentages of each of the two subspecies samples. In the n=53 sample of COAST animals the majority (54,7%) exhibited 12 transverse rows of DCC's on their tails, but three additional results occur in smaller percentages of the *Osteolaemus tetraspis tetraspis* subspecies sample. Similarly, the INTERIOR taxon most frequently (73,4%) has 13 DCC rows transversely crossing its tail when n=15 of the *O. t. osborni* subspecies, but two additional results (12 and 14 rows) were also recorded.

The most predictive positive finding in Chapter 6 was that eleven double-crested caudals occurs only in *O. t. tetraspis*, though only 28,3% of the time in the COAST subspecies (15 positive results out of 53 possible). Thus, the double-crested caudal character fails to be predictive of these two subspecies in *Osteolaemus tetraspis* as a species. However, for those few animals with this result (11 DCC's) the taxonomic question (COAST or INTERIOR) can be answered.

As will be reviewed in Tables 9.9 and 9.10 (below), and also in Figure 9.13 (below), the DCC's can sometimes, but significantly not always, be useful as an indicator of subspecies (COAST and INTERIOR defined the current C.I.T.E.S. way) in *Osteolaemus tetraspis* from the geographic region sampled in this thesis. Note that the relevant geographic division between *O. t. tetraspis* (type locality the Ogowe River in Gabon) and *O. t. osborni* (type locality in the Ubangi River drainage) is the Ogowe-Likouala rivershed divide. As was shown on maps in Chapter 1, the Likouala River is a tributary of the Ubangi, which in turn is a tributary of the Congo River upstream from the cities of Kinshasa and Brazzaville. The whole Ubangi drainage and also the Congo River as far downstream as Kinshasa is defined as INTERIOR, and everything else (theoretically from Cabinda to Senegal) is COAST.

9.2.7 The precaudal rows in Chapter 7 evaluated as a predictor of these two C.I.T.E.S. subspecies

The literature contains no assertions that different ranges of variation occur in the number of thoracic (PC-16-18) precaudal rows on the body, nor is the presence or absence of PC-19 considered by any relevant publication to be diagnostic for these two taxa (*Osteolaemus tetraspis tetraspis* compared with *Osteolaemus tetraspis osborni*). However, the raw data was available, and as a theoretical exercise this thesis examined the “continuous” (a defined term) precaudal rows on the African dwarf-crocodile species in greater detail than most earlier studies, and with a larger known number of specimens. The 2006-2007 expedition’s results included some unexpected examples of low counts of continuous precaudal transverse rows of dorsal scales (PC-16 and PC-17), which occurred only in *O. t. tetraspis* subspecies, when it is defined as the COAST taxon with its traditional C.I.T.E.S. distribution. The most frequent outcome in the 2006-2007 sample was of PC-18 being the anteriormost precaudal thoracic row on the body, as had been predicted by Ross + Mayer (1983:321). The same is true for the predicted and observed frequent occurrence of PC-19 (the optional and posteriormost transverse row of nuchal scales) in the new sample.

Differing from the general and earlier Ross + Mayer (1983) definition of the continuous (not interrupted by spaces of flexible skin) precaudal armour, this thesis established its own modification and enlargement of the possibilities from the earlier PC-1 to PC-18 series (thoracic outcomes PC-16-18), to become the series PC-1 to PC-19, because the posteriormost and optional transverse row of neck scales is visually often a continuation of the body rows, especially when more than one minor transverse space of flexible skin is encountered, as it was (an unexpected result) in this sample of 68 animals. In African dwarf-crocodiles the fold(s) of skin can be deleted from the definition of what the continuous precaudal series means. Otherwise, special *Osteolaemus* circumstances (detailed in Chapter 7) would create false homologies in some of these 68 cases. Displayed as COAST and INTERIOR subspecies taxa, the most relevant results from Chapter 7 are summarized in Table 9.7 (below). Note that PC-16 to PC-18 are combined as one frequency calculation, and PC-19 is independent in this first presentation of Chapter 7 data.

Table 9.7 Testing the theoretical hypothesis that the anteriormost of the 19 possible precaudal rows could identify subspecies when n=68

	O. t. tetraspis	*O. t. osborni*
PC-16	3 out of 53	0 out of 15
PC-17	7 out of 53	0 out of 15
PC-18	43 out of 53	15 out of 15
PC-19	31 out of 53	14 out of 15
Range	16 to 19	18 to 19

Among the traditional choices (PC-16 to PC-18), although low numbers of precaudal rows (PC-16 and PC-17) occur only in the subspecies *O. t. tetraspis* (3+7=10 out of 68 total), the rest of the COAST sample (43 out of 53) have PC-18 as the anteriormost continuous precaudal row on the body. In *O. t. osborni* specimens PC-18 is the anterior end of the continuous precaudal rows (the PC's). Note that PC-19 (a cervical row) is present in both subspecies in large numbers.

Adding the PC-19 transverse row at the base of the neck onto the count of continuous rows on the body in *Osteolaemus tetraspis* is adding two variables together into a new character. In the case of these 68 African dwarf-crocodiles divided geographically into two C.I.T.E.S. subspecies, the PC-19 detail overlaps between both taxa, and PC-18 also can occur in both subspecies. The effectiveness of both methods are equally negatively productive as discriminators of these two geographic races. Neither method works when PC-18 or PC-19 are the result of this count of precaudal transverse rows. The range of PC's is visually presented as a horizontal bar-graph in Figure 9.8 (below).

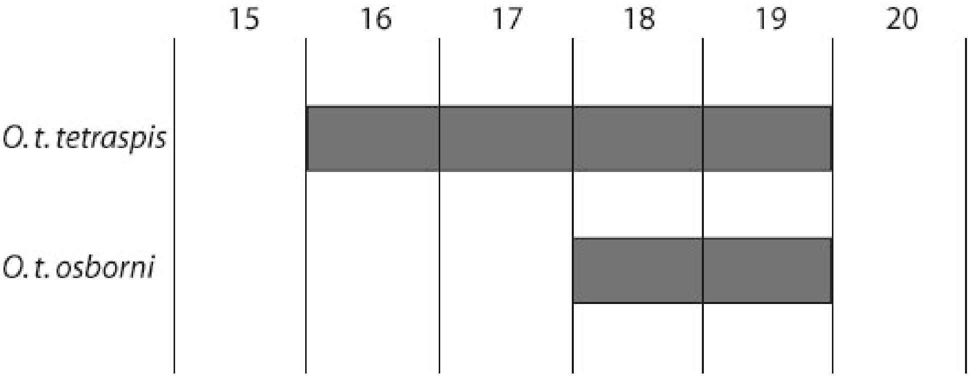


Figure 9.8 Precaudal rows overlap in two taxa of African dwarf-crocodiles

Two precaudal-row results (PC-16 or PC-17 are the most anterior of the continuous series) occur only in *O. t. tetraspis*. Note that PC-18 is a reasonably common outcome in both of these subspecies. This PC-18 finding agrees with the prediction in Ross + Mayer (1983). Also note that PC-19 is present in the majority of this 2006-2007 total (n=68) sample. This was also predicted by Ross + Mayer (1983:321).

Final assessment of the precaudal rows on the body (PC-1 to PC-18, of which 16 and 17 and PC-18 are the thoracic variable), and also the base of the neck (PC-19), as predictors of subspecies in the *Osteolaemus tetraspis* species is presented as a pair of vertical bar-graphs in Figure 9.9 (below).

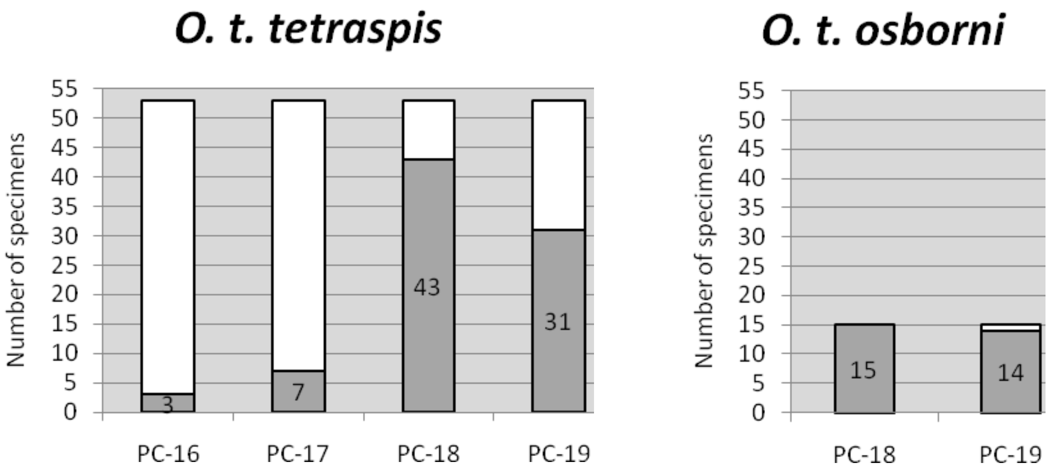


Figure 9.9 Ratio of number of precaudal rows on the body

This figure shows the precaudal rows (both the three relevant thoracic, and the one cervical) in the two compared C.I.T.E.S. subspecies when n=53 *Osteolaemus tetraspis tetraspis* Cope, and n=15 *O. t. osborni* (Schmidt).

With or without PC-19 being included in the continuous precaudal series, the only positive discriminating result in Chapter 7 was that PC-16 and PC-17 are the anteriormost qualifying row in only one taxon. However, the frequency was only 10 out of 53 COAST animals. However, other than the low PC counts (result of 16 and 17 transverse rows), all of the INTERIOR sample had high PC counts (results of 18 or 19 rows), and thus *Osteolaemus tetraspis osborni* overlaps with *O. t. tetraspis*, and in the end (with "continuous" defined either way) it is clear that this general PC's character is not 100% predictive.

In a subjective and practical sense, the special *Osteolaemus* PC count, that includes the 19th precaudal row as a variable, is easier to perform as a method, because close and specialist examination is required for the transverse folds to be seen. However, it is always necessary to find the sacro-caudal juncture (SC-J) before counting the number of precaudal (PC) rows. Therefore, although partly predictive, the continuous PC count has the difficulty factor that locating the SC-J and PC-1 often requires physically handling the animal.

9.2.8 The new permit-free dorsal scalation character in Chapter 8 evaluated as a predictor of these two C.I.T.E.S. subspecies

The 2006-2007 expedition introduced a new scale-count that could possibly identify subspecies (*Osteolaemus tetraspis tetraspis* compared with *Osteolaemus tetraspis osborni*). The 2006-2007 expedition's results about the permit-free scale-count (n=68) included low counts of the permit-free scale-count (27 to 30 rows), and these outcomes occurred only in *Osteolaemus tetraspis tetraspis* when defined as the COAST taxon.

Displayed as COAST and INTERIOR subspecies taxa, two different ways of analysing the permit-free results from Chapter 8 are summarized in Table 9.8 (below). The top two lines of ranges are raw data, while the four lower lines in this table are the percentages of the total count that are anterior to the sacro-caudal juncture.

Table 9.8 The theoretical hypothesis that the permit-free scale-count could identify subspecies, compared with the new data (n=68)

	O. t. tetraspis	*O. t. osborni*
27 to 30 rows	29 out of 53	0 out of 15
31 to 33 rows	24 out of 53	15 out of 15
--- --- --- --- --- ---	--- --- --- --- --- --- ---	--- --- --- --- ---
PC row % < 60%	15 out of 53	13 out of 15
PC row % = 60%	7 out of 53	0 out of 15
PC row % > 60%	18 out of 53	2 out of 15
PC row % > 62%	13 out of 53	0 out of 15

Although low counts (27 to 30 rows) of the permit-free scale-count only occur in *O. t. tetraspis*, the other almost half of this subspecies have 31 to 33 rows. The permit-free count is a composite character that is composed of both PC (precaudal, including PC-19) and DCC (double-crested caudal) numbers. Thus, a percentage of 60% PC rows means 40% DCC rows in the total permit-free count's result. The PC% of the permit-free scale-count is divided into four categories: percentage of PC rows is less than 60%, percentage of PC rows is exactly 60%, percentage of PC rows is slightly more than 60%, and percentage of PC rows is more than 62% of the permit-free scale-count.

The permit-free count is the total number of transverse rows of dorsal scales physically located between the obligate nuchals and the start of the single-crested caudals (see Figure 8.1 above). It is not necessary to locate the dividing line (the SC-J) between the body and the tail, and thus the whole permit-free count can often be relatively easy to record, when compared with determining what percentage of the total character is located anterior to the SC-J. The raw total data from the permit-free count is graphically evaluated as a predictor of subspecies in Figure 9.10 (below).

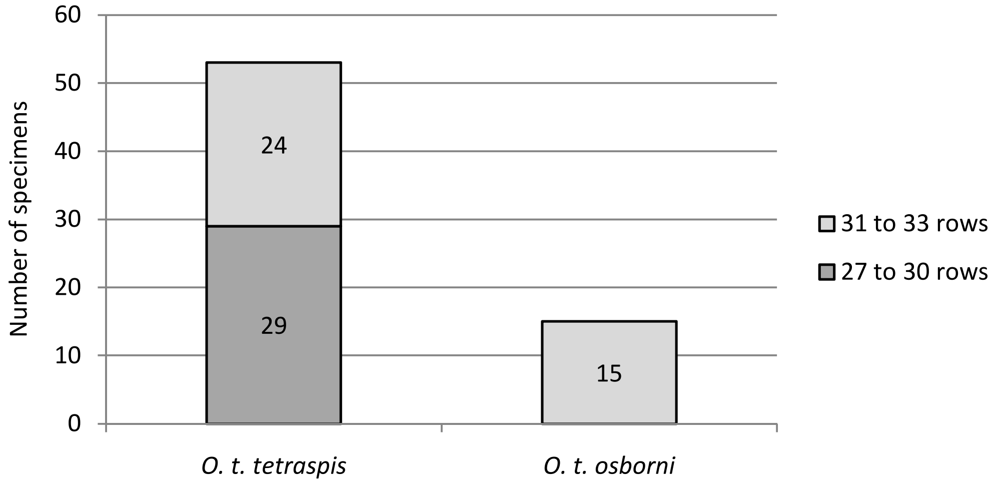


Figure 9.10 Total number of rows present in the permit-free count

All 15 animals from INTERIOR localities, being *Osteolaemus tetraspis osborni*, have 31 to 33 rows in the permit-free scale-count. The results of animals from COAST localities show that "low numbers" of the permit-free scale-count (27 to 30 rows) occur almost in the same frequency as the "high numbers" (31 to 33 rows).

Because the sacro-caudal juncture can be fairly reliably located by the Ross + Mayer (1983) criterion 3 method, and also the criterion 4 way, it is not always necessary to physically handle the African dwarf-crocodile to find the transverse level where the body stops (and the tail starts), but it is always necessary to at least get directly above the animal. Therefore, calculating the percentage of the permit-free count that is PC (precaudal) rows is itself not strictly a permission-free method. However, it is an additional individual way that these two subspecies might be identified, and the results for both taxa are presented as pie-diagrams in Figure 9.11 (below).

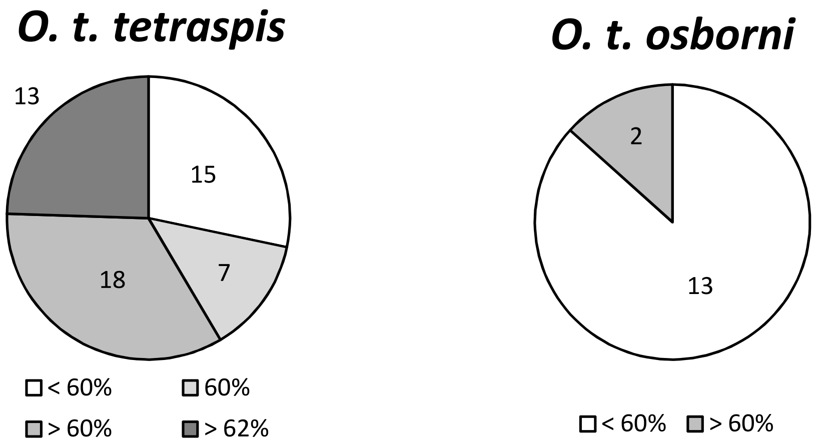


Figure 9.11 PC row % of permit-free count

None of the percentage categories totally characterizes either of the two subspecies. Results of less that 60%, and also greater than 60%, both occur in both taxa. The result of greater than 62% happens only in the COAST sample (n=53), but only in 13 animals. It is more likely that a result of less than 60% will occur in the INTERIOR, but two *Osteolaemus tetraspis osborni* out of 15 had greater than 60% of their permit-free count contributed by precaudal rows (from the SC-J and PC-1 to, and also including PC-19).

The percentages that the combined neck (PC-19) and the body (PC18 to PC-1) contribute to the total permit-free count appears to be less predictive to subspecies than the original data about the number of rows in the total permit-free count. Therefore, considering that the whole count is easier to perform, it is the better of the two Chapter 8 options. The whole count does not require physically being directly above the crocodile, and it does not depend on having the back legs outstretched perpendicular to the body, nor does it require Ross + Mayer's (1983) criteria 1 and 2. Note that in the tables that follow (Tables 9.11, 9.12, and 9.13), the total and raw permit-free scale-count method is reported, and separately the DCC's and PC's are individually reported, but the complicated percentage of the permit-free count that is double-crested caudals or precaudal rows is not presented. This latter percentage analysis was an experiment in this thesis, while what follows is the new 2006-2007 data about characters that have their origin in the already published literature.

9.2.9 Literature assertions reviewed for each subspecies separately

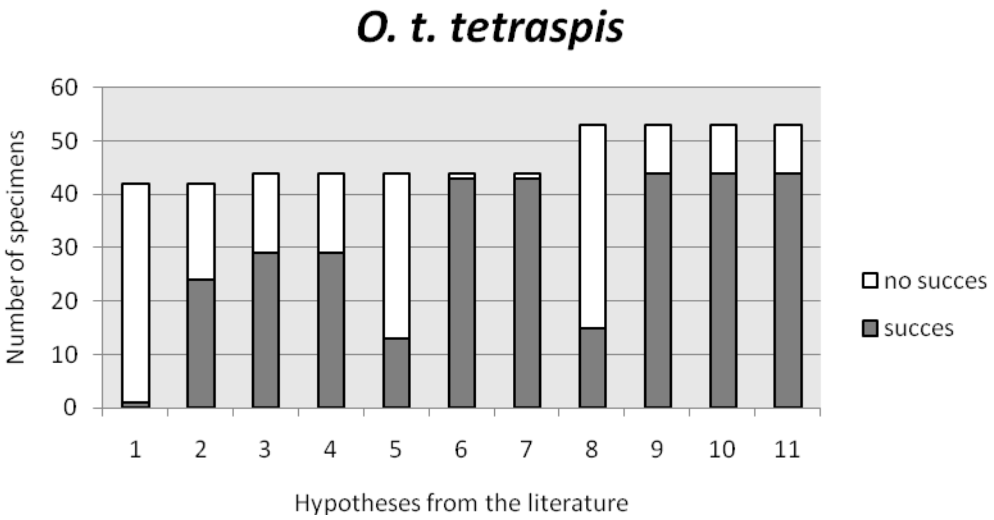
There are approximately a dozen published hypotheses about scalation characters being predictive to subspecies in the African dwarf-crocodile. Each of these literature statements have already been detailed in their relevant chapters, where they were tested for their predictiveness individually as characters, and also collectively for both taxa. In contrast, the tables and figures immediately below are a presentation of identification characters listed collectively, and this time being evaluated for their correct predictive value within only one subspecies. Thus, eleven literature assertions are compared with each other with regard to their success rate at correctly identifying any individual animal in the study sample as *Osteolaemus tetraspis tetraspis* (the COAST subspecies) in Table 9.9 (below).

Table 9.9 Hypotheses from the literature that claim to identify *O. t. tetraspis*, the COAST subspecies

Paper & year	success rate	percentage
Post-occipital scales		
1. Schmidt (1919)	1 out of 42	2,4 %
2. Brazaitis (1973)	24 out of 42	57,1 %
Collar-vent count		
3. Fuchs (1974, 2006)	29 out of 44	65,9 %
4. Charette (1995)	29 out of 44	65,9 %
5. Brazaitis (1973)	13 out of 44	29,5 %
Transverse scale-count		
6. Fuchs (1974, 2006)	43 out of 44	97,7 %
7. Charette (1995)	43 out of 44	97,7 %
Double-crested caudals		
8. Inger (1948)	15 out of 53	28,3 %
9. Brazaitis (1973)	44 out of 53	83,0 %
10. Charette (1995)	44 out of 53	83,0 %
11. Fuchs (2006)	44 out of 53	83,0 %

The literature citations numbered 1-11 actually represent only seven different hypotheses, because four are duplicates. Hypothesis #1 is two transverse PO rows of two scales each; hypothesis #2 is only one transverse row of PO's; hypotheses #3 and #4 are 25-29 transverse rows of ventral scales in the C-V count; hypothesis #5 is 26-27 rows in the C-V count; hypotheses #6 and #7 are 10-12 ventral scales across the widest level of the belly; hypothesis #8 is 11 DCC's; and hypotheses #9, #10 and #11 are 10-12 transverse rows of DCC's.

Some of the hypotheses from the literature work fairly well at correctly identifying the COAST taxon, but none give correct results 100% of the time in this *Osteolaemus tetraspis tetraspis* subspecies. The percentages of success are influenced by the number of COAST dwarf-crocodiles for which the character was recorded, but in all cases the size of the sample is greater than forty *O. t. tetraspis* Cope, 1861 (the Ogowe River in Gabon taxon). The worst literature hypothesis was K.P. Schmidt (1919) about the post-occipital scales in the COAST taxon (2,4% correct in a sample with n=42). However, the best result is one of the two kinds of belly skin characters, and that is good news. Based on the 2006-2007 expedition's sample, it can take 44 specimens of COAST crocodiles to falsify the 10-12 ventral scales across the belly prediction in the literature. If only one specimen was missing, an n=43 sample might have worked 100% of the time for this transverse at widest midbelly-level ventrals character. The COAST taxon's hypotheses are graphed for visual comparison in Figure 9.12 (below).



<u>Figure 9.12 Literature successes at identifying the COAST taxon, *O. t. tetraspis* Cope</u>
In this vertical bar-graph the seven hypotheses (represented by eleven literature citations) from the previous table are plotted for visual comparison. Each vertical bar-column's identification number (1-11, left to right across the bottom) in this figure refers to horizontal lines numbered 1-11 in the preceding table for the COAST subspecies, *Osteolaemus. t. tetraspis* Cope. Thus columns 3 and 4 are exactly the same as each other, and separately columns 6 and 7, and also 9-11 are cases of multiple literature citations to a single identification character.

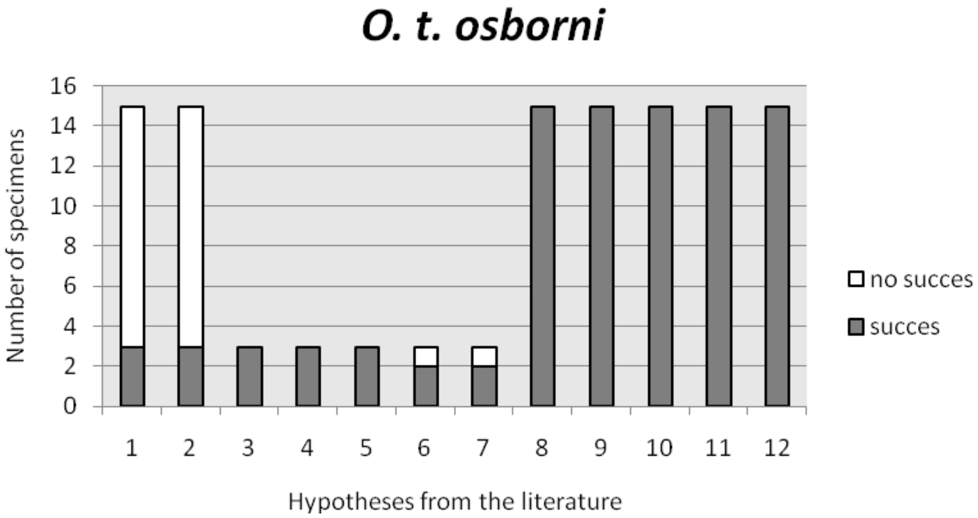
In the immediately preceding figure and table for the *O. t. tetraspis* subspecies, the sizes of the samples (n=always greater than 40 dwarf-crocodiles) is approximately equally representing each of the seven (portrayed as eleven) individual characters. Thus, the ventral scalation data and the dorsal scalation data can be combined as a total group of scale-count literature hypotheses, among which outcomes #6 and #7 (that there are 10-12 ventral scales in the widest row across the belly) are remarkably close to being diagnostic for the COAST taxon. The difficulty factor of needing permission to turn an African dwarf-crocodile onto its back (so that the belly scales can be closely examined) was not a significant problem in the COAST sample, but the same is not true (due to circumstances beyond the expedition's control) for the INTERIOR subspecies, where the total number of animals is smaller (n=15), and the subset from which ventral data was recorded is only three individual specimens (one from Kinshasa, and two from Likouala River). This and other results are reviewed in the comparison of the literature hypotheses about identifying only the *Osteolaemus tetraspis osborni* (Schmidt) subspecies in Table 9.10 (below).

Table 9.10 Literature claims that *O. t. osborni* (Schmidt), the INTERIOR taxon, can be identified

Paper & year	success rate	percentage
Post-occipital scales		
1. Schmidt (1919)	3 out of 15	20 %
2. Brazaitis (1973)	3 out of 15	20 %
Collar-vent count		
3. Fuchs (1974, 2006)	3 out of 3	100 %
4. Charette (1995)	3 out of 3	100 %
5. Brazaitis (1973)	3 out of 3	100 %
Transverse scale-count		
6. Fuchs (1974, 2006)	2 out of 3	66,7 %
7. Charette (1995)	2 out of 3	66,7 %
Double-crested caudals		
8. Schmidt (1919)	15 out of 15	100 %
9. Inger (1948)	15 out of 15	100 %
10. Brazaitis (1973)	15 out of 15	100 %
11. Charette (1995)	15 out of 15	100 %
12. Fuchs (2006)	15 out of 15	100 %

The literature citations numbered 1-12 actually represent only five different hypotheses, because seven are duplicates. Hypotheses #1 and #2 are two transverse PO rows of four scales each; hypotheses #3 and #4 are 22-24 transverse rows of ventral scales in the C-V count; hypothesis #5 is 21-23 rows in the C-V count; hypotheses #6 and #7 are 12-14 ventral scales across the widest level of the belly; and hypotheses #8, #9, #10, #11 and #12 are 12-14 transverse rows of DCC's.

While it was safe to compare various dorsal characters with other ventral characters in the earlier COAST subspecies (where sample-size was always greater than 40 animals), this is not true here in the INTERIOR sample. Rather, the two kinds of dorsal character hypotheses (the PO's and the DCC's) form a group of *O. t. osborni* where n=15, while the alternative group of literature hypotheses is the two kinds of ventral characters with n=3 for the same *O. t. osborni* (Schmidt) taxon. This discrepancy between sample sizes among identification characters from the literature is visually presented as a vertical bar-diagram in Figure 9.13 (below).



<u>Figure 9.13 Literature successes at identifying the INTERIOR taxon, *O. t. osborni* (Schmidt)</u>

The numbers 1-12 across the bottom of this figure represent the characters (literature hypotheses) with the same identifying numbers from the adjacently preceding table. There are some 100% successes in characters where n=15 African dwarf-crocodiles from the INTERIOR, and there are also some 100% successes in the n=3 group of characters. However, even when 15 out of 15 INTERIOR specimens agree, it is still less impressive than 40 out of 40 COAST crocodiles, and 3 out of 3 *Osteolaemus tetraspis osborni* (Schmidt) is least impressive of all.

Individual subspecies tables and figures have shown that one literature hypothesis (the transverse count across the belly) works well in the COAST subspecies, but not as well in the INTERIOR taxon. Similarly, one literature hypothesis (the collar-vent count) works well in one subspecies (INTERIOR), but not as well in the other (COAST) taxon. Both of these ventral scalation characters are very important for identifying commercial belly-hides (ventral skins), and thus it is a great disappointment that the n=3 sample-size factor makes it statistically incorrect to compare results between samples that have such remarkably different numbers of specimens. Therefore, because there is such overwhelming ambiguity about ventral counts in the INTERIOR, these two kinds of scalation characters (the C-V count of rows, and the transverse count of ventral scales at midbelly level) cannot be further compared with the various kinds of dorsal scalation characters such as the double-crested caudals, and the post-occipital scales, and others.

There is a joke (a common expression, and a wise observation) about how every good thesis concludes with a recommendation that additional research is needed. However, it is absolutely true that both kinds of ventral counts show promise as at least partly helpful identification tools, but in this case the INTERIOR sample recorded by the 2006-2007 expedition is unfortunately too small to prove it. Thus, the simplified generalization (that none of the scalation characters examined in this thesis works 100% of the time) has the notable exception that more work is needed on the ventral pair (the C-V and transverse ventrals), both of which are included in the 1995 identification manual for C.I.T.E.S. crocodilians. The highest general priority is INTERIOR animals, and when examining them, the obligate nuchals can sometimes have fusions that should be recorded in detail. Further, whenever possible it is vital that the two kinds of ventral counts are carefully investigated. The King + Brazaitis (1971) method is recommended, and it is cautioned that both of these ventral characters must be clearly defined. The collar-vent count requires finding the limits of the collar and the vent (both of which require specialist definitions), and the transverse belly-count requires finding the limits of the truly “ventral” kind of scales.

9.3 CONCLUSION

9.3.1 Defining the ultimate question

Because of the very small sample of ventral data from the smallish sample of *Osteolaemus tetraspis osborni* (the INTERIOR taxon), the two kinds of ventral characters have now (immediately above in this chapter) been deleted from further consideration in the formal evaluation that follows. However, it is still theoretically possible that the collar-vent (C-

V) count and the transverse ventral scales count (across the belly at its widest level) are in fact supporters of the hypothesis that *Osteolaemus tetraspis osborni* (Schmidt) is identifiable by its scalation. The 2006-2007 expedition had hoped to report on more than forty INTERIOR animals, but significant safety (and other relevant) circumstances caused the available time in the relevant region (in this case the Brazzaville market as a sample of Likouala River animals) to be unexpectedly limited. Therefore, the question becomes an evaluation of the utility of only the dorsal scalation characters, because the ventral scalation needs further investigation. However, it is noteworthy that the C-V count gives correct results at finding *O. t. tetraspis* more than 50% of the time when n=44 *Osteolaemus tetraspis tetraspis* Cope.

When the two belly-skin characters are removed from consideration, there are seven kinds of dorsal characters that remain to be evaluated for their degree of support for the COAST and INTERIOR taxonomic division. The final comparison of available characters will involve three tables. First, the percentages of success at finding the correct identification within the COAST category (*O. t. tetraspis*), and second the same thing in the INTERIOR category (*O. t. osborni*), and lastly the correct predictive percentage for the whole total sample with both COAST and INTERIOR animals in it. Each of the dorsal scalation characters has a percentage of correctness for its own subspecies "only" (examination restricted to one subspecies), as shown for only the COAST sample in Table 9.11 (below).

Table 9.11 Actual COAST crocodiles correctly identified by scalation characters

Scale-count character	frequency	percentage
Post-occipital scales	4 out of 42	9,5%
Big nuchal scales	6 out of 47	12,8%
Presence PC-19	0 out of 53	0,00%
Sacro-caudal juncture	0 out of 53	0,00%
Double-crested caudals	15 out of 53	28,3%
Precaudal rows	10 out of 53	18,9%
Permit-free count	29 out of 53	54,7%

In the contest for the single dorsal scalation character that is most often predictive about COAST animals, the permit-free count is the winner. In a sample of 53 geographically identified COAST crocodiles, the results from the new permit-free method agreed 29 times, giving it a 54,7% success rate. Although deleted from the final consideration (and not included in this table) due to insufficient data about the alternative subspecies, note that the ventral scale-count across the belly was able to identify only 5 out of 44 COAST dwarf-crocodiles correctly (an 11,4% success rate). More impressive, though, was the collar-vent method, which worked 27 out of 44 times, giving a 61,4% score.

Although the permit-free count agrees with COAST geography more than 50% of the time (and in this subspecies the C-V count also works more than half the time), the probability of an *Osteolaemus t. tetraspis* being correctly identified to subspecies is always significantly less than the 100% certainty that this thesis has been seeking. However, identifying *O. t. tetraspis* correctly is only part of the problem, because there is the related question about how many known (by geography) INTERIOR animals are correctly identified to subspecies. This latter choice of characters within only *O. t. osborni* is presented in Table 9.12 (below).

Table 9.12 Actual INTERIOR crocodiles correctly identified by scalation characters

Scale-count character	frequency	percentage
Post-occipital scales	0 out of 15	0,00%
Big nuchal scales	0 out of 14	0,00%
Presence PC-19	0 out of 15	0,00%
Sacro-caudal juncture	0 out of 15	0,00%
Double-crested caudals	0 out of 15	0,00%
Precaudal rows	0 out of 15	0,00%
Permit-free count	0 out of 15	0,00%

In this taxonomic case in the game of correctly recognizing its known geographic subspecies, when it is the INTERIOR taxon *Osteolaemus tetraspis osborni* K.P. Schmidt, 1919, originally described as *Osteoblepharon osborni* Schmidt (new genus and new species), there is no character that is a winner. Each of the seven kinds of dorsal scalation characters fails 100% of the time in *O. t. osborni* (Schmidt). Thus, in the INTERIOR sample the permit-free method is not more predictive than any of the other characters being considered in this final single subspecies comparison. Note that in this INTERIOR subspecies the two ventral characters correctly predicted their actual geographic taxon zero out of three times, which is 0,00% success, and 100% failure.

Both of the preceding two tables were samples of one or the other subspecies being analysed by itself. The COAST sample is considerably larger (more numerous) than the INTERIOR sample, and this disproportionality in the comparative numbers of specimens has probably influenced the results to some degree. In theory it is easier to achieve a zero percentage of success when n=15 INTERIOR than when n=53 COAST. Thus, because the sample-size can be increased by adding the two subspecies together, the seven kinds of dorsal scalation characters are now subjected to the same evaluation and comparison, when n=68 African dwarf-crocodiles in the species *Osteolaemus tetraspis* Cope, in Table 9.13 (below).

Table 9.13 Subspecies predictiveness ratings of dorsal scalation characters when n=68 (the whole sample)

Scale-count character	frequency	percentage
Post-occipital scales	4 out of 57	7,02%
Big nuchal scales	6 out of 61	9,84%
Presence PC-19	0 out of 68	0,00%
Sacro-caudal juncture	0 out of 68	0,00%
Double-crested caudals	15 out of 68	22,06%
Precaudal rows	10 out of 68	14,70%
Permit-free count	29 out of 68	42,65%

The permit-free count is the winner. In this and other characters, the total results in this taxonomically combined comparison of 68 animals fairly closely repeat the general pattern of results from the COAST only sample, because the INTERIOR sample is smaller. Note that 27 out of 47 combined animals had C-V counts that worked (57,45%), and 5 out of 47 transverse ventral counts worked (10,64%), and thus these latter two characters also exhibit this trend.

The inquiry into which individual character works the best in now finished. The permit-free count is better than any of the other dorsal characters, and it remains possible that there is one kind of ventral count that works even better, but none of the characters tested in this thesis was able to produce results that are trustworthy for the whole Zoer 2006-2007 sample of *Osteolaemus tetraspis* Cope.

9.3.2 The question is clear, now the answer

The contest to see which of the various characters works the best was instructive. Especially one of the C.I.T.E.S. ventral identification characters works sometimes, and the dorsal scalation permit-free character also works sometimes, but they fail to predict their geographic taxon too much (about 40% or more) of the time to be relied upon when 100% reliable subspecies identification is required. The question is not about what kind of scale-count character, but rather about all of the different kinds as a combined total study. Thus, African dwarf-crocodile scalation characters as a collective group are the real subject (distinguished from subjects like cranial measurements, coloration, DNA, and the degree of boniness of the septum between the two nostrils). There appears to be no 100% reliable way that scalation supports the *Osteoblepharon osborni* Schmidt hypothesis. Thus, African dwarf-crocodile scale-counts in general do not support the current taxonomic separation of *Osteolaemus tetraspis* Cope into two subspecies when the second taxon is *O. t. osborni* (Schmidt, 1919).

9.3.3 Subjective analysis and afterword

In an objective and mathematical sense, the INTERIOR taxon, *Osteolaemus tetraspis osborni* (Schmidt) is not strongly supported by scale-count characters. However, the actual number of INTERIOR animals in the 2006-2007 sample was significantly smaller than the number of COAST crocodiles. It was concluded that additional research is needed before the total ranges of variation in several characters (notably the two kinds of ventral counts) are reliably known. Thus, in a subjective sense, the belly becomes a special problem on its own. This is also true about fusions of obligate nuchal scales, a new phenomenon in *Osteolaemus* that is probably unknown to science, and is definitely deserving of further attention. The presence or absence of fused nuchals could possibly be strongly correlated with one or the other of the two taxa, but again the small number of INTERIOR animals significantly weakens any conclusion at this time.

There were three kinds of reasons why the INTERIOR sample was not more than forty *O. t. osborni* (Schmidt). First, there were national permits that had starting and stopping dates, and there was nothing to be gained by gathering data that could not be later published and shared with science. Second, there was political unrest in the region (the election in the DRC made Kinshasa and Brazzaville somewhat unsafe), and thus the examination of Likouala River animals in the Brazzaville market was prematurely ended at n=14, as opposed to the desired n=40 or more *O. t. osborni* specimens.

The third reason for the INTERIOR sample of African dwarf-crocodiles being so small is the local permission required inside the bushmeat trade in the whole general region. Whenever possible, the expedition had appropriate national permits in its possession, but official research permits were of no utility in market situations. In contrast, the showing or mentioning of a government document would normally cause the owners of crocodile bushmeat to hide it. However, being careful to appear to be tourists, it was possible to examine dwarf-crocodiles in markets to a limited degree. The limiting factor was gaining permission to closely examine someone else’s food. The bushmeat seller in Figure 9.14

(below) knew where his COAST animal was collected from the wild, and he was personally willing to hold it for these photos (taken by a local friend of his), but a proper scientific examination was completely out of the question.

Figure 9.14 Dorsal and ventral views of bushmeat *Osteolaemus*

Vendor at Pointe-Noire market (Congo-Brazzaville nation) exhibits fresh protein source for human consumption.

The alternative to bushmeat markets is catching dwarf-crocodiles and examining them when conditions for scientific study are available. The photos in Figure 9.15 (below) show some wild juvenile *Osteolaemus* being examined before they were later released at their individual places of origin.

Figure 9.15 Proper conditions for carefully examining African dwarf-crocodiles

With permission from the local chief, wild *Osteolaemus* were collected from the forest at night by the expedition itself, and then the crocodiles were examined at leisure the following day before being released back at their place of capture (near Pointe-Noire in Congo-Brazzaville, on the coast).

The permit-free count of defined transverse rows of dorsal scales has the subjective factor that it is the easiest of the possibly meaningful hypotheses that can later be tested with additional specimens.

Afterword

During the advanced stages of writing this thesis, back in March 2009, a new and relevant paper was published by Eaton, M., Martin, A., Thorbjarnarson, J., and Amato, G. in the journal *Molecular Phylogenetics and Evolution* (not yet seen), and an earlier abstract was released on the internet in November 2008 (seen), and also in 2008 the abstract was printed in the *Crocodile Specialist Group Newsletter* 27(4):20 (seen). Based on the abstract of Eaton *et al*. (2009): Species-level diversification of African dwarf crocodiles (genus *Osteolaemus*): a geographic and phylogenetic perspective. *Mol. Phylogenet. Evol.* 50(3):496-506, there are two factors that are directly relevant to this thesis. First, the geographic border where the Eaton *et al*. COAST and INTERIOR taxa are divided from each other is effectively the same as the taxonomic border employed in this thesis. There is no conflict about what is COAST and what is INTERIOR in this region of Africa. The Ogowe River is COAST, and the Likouala River is INTERIOR. The second factor proves that the taxonomic question is still relevant. The Eaton *et al*. paper agrees that *osborni* Schmidt is INTERIOR and that *tetraspis* Cope is COAST, but these two geographic groups have been newly elevated from being hypothetical subspecies to now be proposed as the hypothetical species pair *Osteolaemus osborni* (Schmidt) and *Osteolaemus tetraspis* Cope.

BIBLIOGRAPHY

BRAZAITIS, P. 1973. The identification of living crocodilians. *Zoologica* (New York), 58 (4): 59-101.

CHARETTE, R. 1995. *CITES identification guide – crocodilians. Guide to the identification of crocodilian species controlled under the Convention on International Trade in Endangered Species of Wild Fauna and Flora.* Ottawa, Ontario, Canada: Minister of Supply and Services, colour coded pagination.

COPE, E.D. 1860 (1861). List of the recent species of emydosaurian reptiles in the museum of the Academy of Natural Sciences. *Proceedings of the Academy of Natural Sciences of Philadelphia* 1860 (12): 549-550.

FREY, E. 1988a. Anatomie des Körperstammes von *Alligator mississippiensis* Daudin (Anatomy of the body stem of *Alligator mississippiensis* Daudin). *Stuttgarter Beiträge zur Naturkunde*, Ser. A (Nr. 424): 1-106.

FREY, E. 1988b. Das Tragsystem der Krokodile – eine biomechanische und phylogenetische Analyse (The carrying system of crocodilians – a biomechanical and phylogenetical analysis). *Stuttgarter Beiträge zur Naturkunde*, Ser. A (Nr. 426): 1-60.

FUCHS, K. 1974. *Die Krokodilhaut*; *Ein wichtiger Merkmalträger bei der Identifizierung von Krokodil-Arten*. Darmstadt, Germany: Eduard Roether Verlag, 183 pp.

FUCHS, K. 2006. *The crocodile skin, important characteristics in identifying crocodilian species.* Frankfurt am Main, Germany: Edition Chimaira, 175 pp.

GRAY, J.E. 1867. Synopsis of the species of recent crocodilians or emydosaurians, chiefly founded on the specimens in the British Museum and the Royal College of Surgeons. *Transactions of the Zoological Society of London*, Volume VI (paper VII): 125-169 + Pls. 31-34.

INGER, R.F. 1948. The systematic status of the crocodile *Osteoblepharon osborni*. *Copeia* 1948 (1): 15-19.

KING, F.W. & Brazaitis, P. 1971. Species identification of commercial crocodilian skins. *Zoologica* (New York), 56 (2): 15-75.

MURRAY, A. 1862. Description of *Crocodilus frontatus*, a new crocodile from Old Calabar River, West Africa. *Proceedings of the Scientific Meetings of the Zoological Society of London*, Volume 1862: 213-218 + Pl. XXIX.

ROMER, A.S. 1956. *Osteology of the reptiles.* Chicago & London: The University of Chicago Press, xxi + 772 pp.

ROSS, F.D. & Mayer, G.C. 1983. On the dorsal armor of the Crocodilia, pp. 305-331 in: A.G.J. Rhodin and K. Miyata (eds.), *Advances in herpetology and evolutionary biology*. Cambridge Mass: Museum of Comparative Zoology, xx + 725 pp.

SCHMIDT, K.P. 1919. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1905-1915. Part I. Turtles, crocodiles, lizards, and chameleons. *Bulletin of the American Museum of Natural History*, 39 (2): 385-624, Pls. 7-32 + maps.

THORBJARNARSON, J. & Eaton, M. 2003. Crocodile surveys (Congo & Gabon). Crocodile Specialist Group Newsletter, Volume 22 (3): 6-8.

THORBJARNARSON, J. & Eaton, M. 2004. Preliminary examination of crocodile bushmeat issues in the Republic of Congo and Gabon, pp. 236-247 in: *Crocodiles: proceedings of the 17th Working Meeting of the Crocodile Specialist Group*. Darwin, Northern Territory of Australia, 24-29 May 2004, xxvi + 530 pp.

VILLIERS, A. 1958. *Tortues et crocodiles de l'Afrique noire francaise*. Dakar, Senegal: Institute Francaise d'Afrique Noire, Initiations Africaines (No. 15), 354 pp.

WERWUTH, H. & Fuchs, K. 1983. In P. Dollinger (ed.), *Convention on International Trade in Endangered Species of Wild Fauna and Flora*, *Identification manual*, Volume 5: parts and derivatives II (crocodilians). Gland, Switzerland: Secretariat of the Convention IUCN.

ABSTRACT

African dwarf-crocodile scale-counts evaluated as supporters of *Osteolaemus tetraspis osborni*
(Reptilia, Crocodylia, Crocodylidae)
by
Rogier de Boer
Study leader: Prof. W. van Hoven
Degree: Master of Science in Wildlife Management

The Convention on International Trade in Endangered Species of Wild Fauna and Flora (C.I.T.E.S.) has always recognized *Osteolaemus tetraspis osborni* (Schmidt, 1919) as a geographic subspecies of the African dwarf-crocodile, taxonomically distinguished from the subspecies *Osteolaemus tetraspis tetraspis* Cope, 1861. These two subspecies are primarily based on anatomical evidence that is not visible on a whole living animal. The subspecies distinction is the internal degree of boniness of the septum between the two external nostrils. This character must be examined by dissection of the animal's head. Therefore it is desirable that some reliable and diagnostic kind of externally visible identification character (such as coloration, measuring head proportions, or counting scales) should be searched for. Otherwise, any individual *Osteolaemus tetraspis* animal must be partly dissected to see what subspecies it is.

In this thesis, approximately a dozen different external characters (mostly counting scales or rows of scales) are independently tested and compared with each other in an effort to determine which of them is the most useful as an identification tool for separating the *Osteolaemus t. osborni* subspecies from the *O. t. tetraspis* taxon. If none of these scalation details are found to be 100% reliable as a predictor of the appropriate geographic taxon, then some additional factors become relevant, such as their comparative difficulties in physically performing the investigation. Some kinds of scale-counts are easier to define and record than others.

The new sample is 68 African dwarf-crocodiles, of which 53 are geographically in the COAST (*O. t. tetraspis*) taxon, and 15 are from the INTERIOR (*O. t. osborni*). The data was collected by field-work in numerous African nations, and the expedition sampled and travelled across the C.I.T.E.S. subspecies boundary between these two taxa in several ways. In comparison with earlier published reports about scalation characters in the *Osteolaemus tetraspis* species, this new sample is relatively large, and has remarkably good precision about locality data. Further, this expedition (the Zoer *Osteolaemus* Project, 2006-2007) exercised extreme care to apply clear definitions for the various characters (scale-counts, row-counts, etc.).

Based on good samples, and on the high quality scalation data collected in 2006-2007 in Africa, it is concluded that none (zero) of these dorsal and ventral skin characters (with the possible exception of the two kinds of ventral scale-counts, for which the INTERIOR sample was only 3 animals) yield satisfactory results for discriminating subspecies of dwarf-crocodiles in the general part of the continent that was examined. All of these many kinds of scalation features fail to 100% reliably predict the correct subspecies (COAST or INTERIOR) outcome. Some characters never (0,00%) work, while other characters work part of the time, but not one gives the level of predictability that is required by C.I.T.E.S. for quick and accurate taxonomic identification in *Osteolaemus tetraspis* with these two subspecies as regulated taxa.

All of the literature scalation characters required detailed special examination procedures, usually involving physically handling the animal. This thesis invents and recommends a new kind of character which has the advantage that just looking at the dorsal surface of the crocodile is often sufficient, and sometimes it can be done through a telescope. For this "permit-free" scalation character, properly taken photographs can include the normal (tourist at the zoo) view from the side and slightly above. It is not necessary to look straight down at the animal, as long as the number of transverse rows on the base of the neck, and along the length of the body, and on the proximal half of the tail can be counted.

Neither the old nor the new characters work 100% of the time, and although the permit-free count of transverse rows on the dorsum is slightly more predictive than any of the others, even this new method yields remarkably poor results. However, given a large enough sample (for example bushmeat or stuffed animals or flat hornback hides passing through a local market over a long period of time), it is predicted that an interesting indication of subspecies identification could, in a statistical way, possibly be obtained. In the final analysis, though, African dwarf-crocodile scale-counts do not appear to support the model of two taxa in *Osteolaemus tetraspis* as a species, and therefore they do not support the inclusion of *Osteolaemus tetraspis osborni* as a regulated taxon on the C.I.T.E.S. list of crocodilians.

UITTREKSEL (EKSERP)

Evaluatie van schubbentellingen van de Afrikaanse dwergkrokodil, die bijdragen in de erkenning van *Osteolaemus tetraspis osborni* (Reptilia, Crocodylia, Crocodylidae)
door
Rogier de Boer
Studie leider: Prof. W. van Hoven
Graad: Master of Science in Wildlife Management

Het CITES verdrag ("Convention on International Trade in Endangered Species of Wild Fauna and Flora") heeft *Osteolaemus tetraspis osborni* (Schmidt, 1919) altijd erkent als een geografische ondersoort van de Afrikaanse dwergkrokodil, die onderscheiden kan worden van *Osteolaemus tetraspis tetraspis* Cope, 1861. Deze twee ondersoorten zijn primair gebaseerd op anatomisch bewijs dat niet zichtbaar is op een puntgaaf en levend dier. Het onderscheid tussen de ondersoorten is de interne graad van het aanwezig bot van de afscheiding tussen de twee uitwendige neusgaten. Dit karakter zal moeten worden onderzocht middels een autopsie op het hoofd van het dier. Daarom is het wenselijk dat er gezocht wordt naar een aantal betrouwbare en diagnostieke vormen van uitwendig zichtbare identificatie karakters (zoals kleuring, het meten van hoofdproporties, of het tellen van schubben). Zo niet, dan zal ieder individueel *Osteolaemus tetraspis* dier gedeeltelijk moeten worden ontleed om te zien welke ondersoort het betreft.

In deze scriptie zijn ongeveer een twaalftal verschillende uitwendige karakters (met name het tellen van schubben of rijen van schubben) onafhankelijk van elkaar getest en onderling vergeleken in een poging om vast te stellen welke van hen het meest bruikbaar is als een middel ter identificatie voor het onderscheiden van de *Osteolaemus t. osborni* ondersoort en de *O. t. tetraspis* taxon. Wanneer geen van deze schubbenkleed details als 100% betrouwbaar wordt beschouwd als voorspeller van de van toepassing zijnde taxon, dan worden een aantal aanvullende factoren relevant, zoals de moeilijkheidsgraad van de fysieke uitvoering van het onderzoek. Sommige schubbentellingen zijn eenvoudiger te definiëren en te registreren dan andere.

De nieuwe sample bestaat uit 68 Afrikaanse dwergkrokodillen, waarvan er 53 geografisch gezien in de KUST (*O. t. tetraspis*) taxon zitten en er 15 zijn van het BINNENLAND (*O. t. osborni*). De gegevens zijn verzameld middels veldwerk in een groot aantal Afrikaanse landen en de expeditie verzamelde op verscheidene manieren gegevens van deze taxa aan beide zijden van de C.I.T.E.S. ondersoorten grens. In vergelijking met eerder gepubliceerde

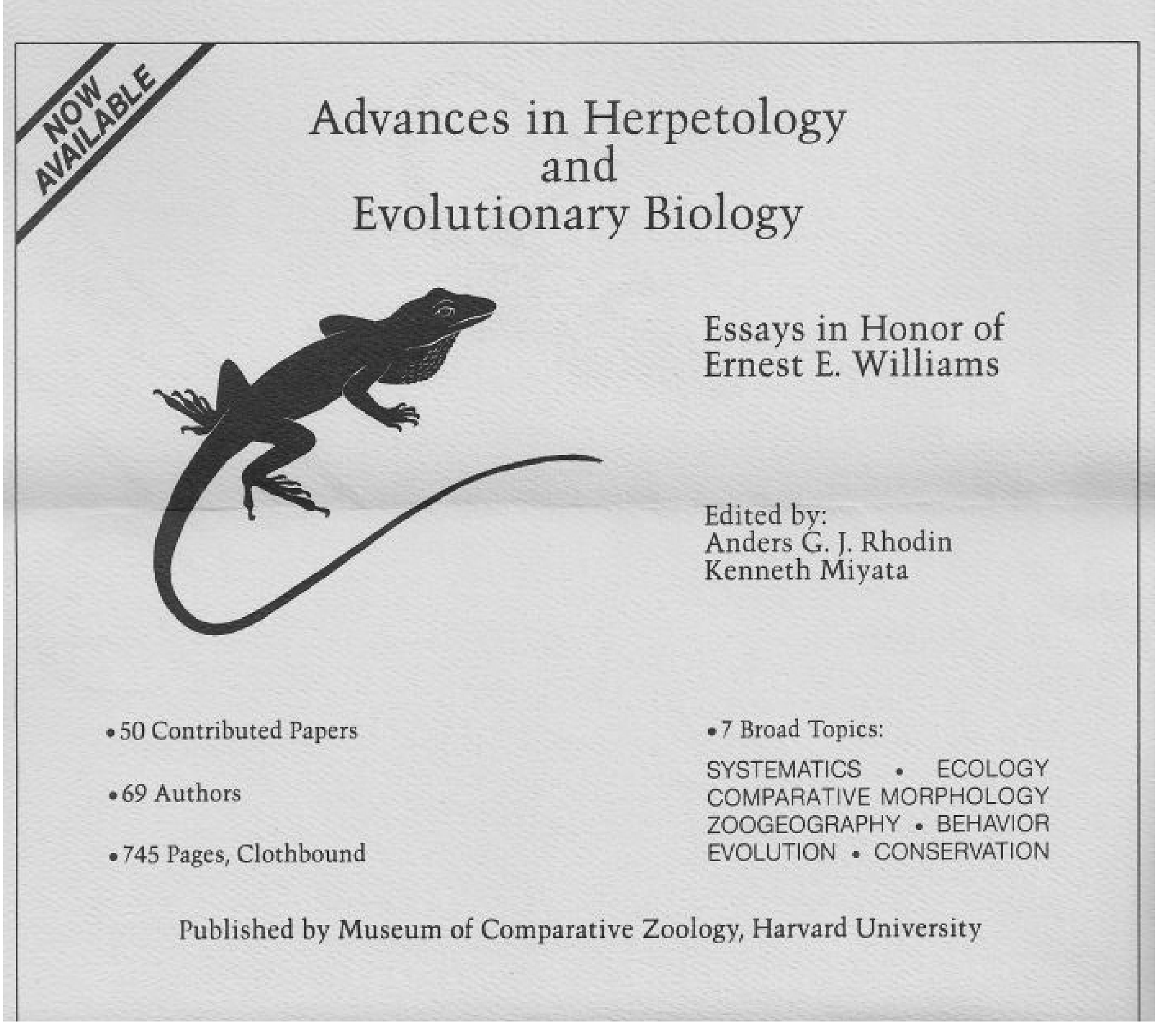
rapporten over schubbenkleed karakters in de soort *Osteolaemus tetraspis*, is deze nieuwe sample relatief groot en heeft het opvallend nauwkeurige plaatsgegevens. Verder heeft deze expeditie (het Zoer *Osteolaemus* Project, 2006-2007) voor zeer duidelijke definities gezorgd voor de verschillende karakters (schubbentellingen, rij-tellingen, enz.).

Op basis van goede samples en de hoge kwaliteit van de in 2006-2007 in Afrika verzamelde schubbenkleed gegevens, kan worden geconcludeerd dat geen (nul) van deze rug en buik huidkarakters (met mogelijk uitzondering van de twee schubbentelllingen op de buik, waarvan de BINNENLAND sample slechts 3 dieren was) bevredigende resultaten geeft om ondersoorten in dit breedvoerig onderzochte deel van het continent te kunnen onderscheiden. Al deze schubbenkleed kenmerken schieten te kort om 100% betrouwbaar de juiste ondersoort te voorspellen (KUST of BINNENLAND). Sommige karakters werken nooit (0,00%), andere gedeeltelijk, maar geen enkele geeft het door C.I.T.E.S. vereiste niveau van voorspelbaarheid voor een snelle en accurate identificatie van *Osteolaemus tetraspis* met deze twee ondersoorten als gereguleerde taxa.

Alle schubbenkleed karakters uit de literatuur vereisten gedetailleerde en speciale onderzoeksprocedures, waaronder vaak het fysiek hanteren van het dier. Deze scriptie vindt uit en beveelt aan een nieuw karakter, welke het voordeel heeft dat enkel het kijken naar de bovenkant van de krokodil voldoende is en soms met behulp van een verrekijker kan gebeuren. Voor deze “vergunning-vrije” schubbenkleed karakter kunnen fatsoenlijk genomen foto’s het normale (toerist in een dierentuin) aanzicht weergeven van de zijkant en lichtelijk van boven. Het is niet nodig om recht boven het dier naar beneden te kijken, zolang het aantal rijen van de basis van de nek in de lengterichting van het lijf tot ongeveer de helft van de staart kunnen worden geteld.

Noch de oude, noch de nieuwe karakters werken in 100% van de gevallen en ondanks dat de “vergunning-vrije” telling van dwars op de bovenkant van het dier lopende rijen een iets betere voorspelling geeft dan alle andere, heeft zelfs deze nieuwe methode opvallend slechte resultaten. Echter, met een sample die groot genoeg is (bijvoorbeeld “bushmeat” of opgezette dieren of huiden, die over een lange periode op lokale markten worden verhandeld) ligt het in de lijn der verwachting dat er een interessante indicatie voor de identificatie van ondersoorten (op een statistische manier) kan worden verkregen. Al met al kan worden gezegd dat schubbentellingen in Afrikaanse dwergkrokodillen niet het model van twee taxa in *Osteolaemus tetraspis* ondersteunen en daarmee *Osteolaemus tetraspis osborni* niet erkennen als een gereguleerd taxon in de C.I.T.E.S. lijst van krokodillen.

ANNEXURE A – ROSS + MAYER (1983) REPRINTED



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On the Dorsal Armor of the Crocodilia

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GREGORY C. MAYER[2]

ABSTRACT. A new method for counting the scales of the dorsal armor of crocodilians is introduced. Based on the one-to-one correspondence between vertebrae and transverse scale rows, it allows comparisons between species on the basis of homologous scale rows. Scale rows are counted away from the evolutionarily conservative sacro-caudal juncture in precaudal and caudal series, approaching the more variable anterior and posterior ends of the dorsal armor from a fixed central point. Primitively, crocodilian dorsal armor consists of 27 transverse precaudal rows of two scutes each, as is found in protosuchians. Changes occurring in the evolution of the modern crocodilians are 1) broadening of the trunk armor; 2) breakup of the ancestral scute pair into many elements per transverse row; 3) loss of the anteriormost transverse rows; and 4) narrowing the armor at the cervico-thoracic juncture. Descriptions of the dorsal armor and its variation in all living species are given. The most frequent kinds of variation in the living crocodilians, both among and within species, are the deletion of transverse rows and the compounding of transverse rows in the cervical region. *Gavialis* is the most primitive living species, departing least from the mesosuchian type of armor, while *Crocodylus acutus* and *C. porosus* are the most derived, showing great reduction from the primitive eusuchian pattern in both trunk and cervical regions.

INTRODUCTION

> Nothing is more fugitive than the forms of crocodiles. —Geoffroy, *in* Cuvier, 1831.

Our methodological and conceptual approach to the dorsal armor of the living Crocodilia differs from that of most previous authors (Cuvier, 1807; Duméril and Bibron, 1836; Boulenger, 1889; Deraniyagala, 1939; Wermuth, 1953; Brazaitis, 1973), but follows directly from insights available in the morphological and paleontological literature (Huxley, 1859; Colbert and Mook, 1951; Nash, 1975). Since the latter part of the eighteenth century, crocodile taxonomists have described dorsal armor from the anterior end first. The traditional methodology involves counting scales (scutes) from occiput to tail tip in terms of postoccipitals, nuchals, dorsals and caudals. The difficulty with counting in this way is that the greatest and most interesting variation occurs in the form of missing, enlarged and fused transverse scale rows in the cervical region. This being the case, the most outstanding variation is encountered initially, resulting in unreliable and oftentimes false homologies. By not establishing the relationships among the sacrum, hind legs, and dorsal armor, various authors have counted the dorsals and caudals beginning or ending with any of several scale rows. We find it interesting and heartening, though, that our conclusions generally agree with those of the traditional method, and that we have little evidence to suggest that the current classification of the living Crocodilia is incorrect.

Our method considers the transverse scale rows on the body and tail in relation to the underlying vertebrae, with which there is primitively a one-to-one relationship. There is always an unarmored space immediately behind the head in living species, and there may be one or two more such spaces near the anterior

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end of the series; but, invariably, there is a continuous series of transverse rows from the region of the shoulders, over the sacrum, and on to the tip of the tail. These transverse rows of bone and scale correspond one-to-one with immediately underlying vertebral elements. Huxley (1859) first observed the one-to-one correspondence in *Caiman crocodilus*, and explained that, "the anterior part of the inner surface of each of the two middle scutes is connected by a ligament with the extremity of the spinous process of a vertebra; at least this is the case in the dorsal, lumbar, sacral, and anterior caudal regions." Our counts are made from the evolutionarily conservative sacro-caudal juncture. We approach the more variable anterior and posterior ends of the dorsal armor from a fixed central point, which is the same for all living and fossil species.

Each transverse row is intervertebral in position, the median elements of a row being attached to the neural spine of the anterior vertebra, and extending posteriorly to overlap the one behind. The dorsal armor thus exhibits the primary segmentation which exists prior to resegmentation in the development of the vertebral column (Williams, 1959). Seidel (1979) observed that the blood supply to the transverse rows of dorsal armor on the body of *Alligator mississippiensis* is by means of a series of unpaired arteries, the dorsal median arteries, which emerge through the deep fascia between successive neural spines, and which also supply the neural spine of the anterior vertebra. All osteoderms in a transverse row and the neural spine of the vertebra anterior to the row receive blood from a common source. Transverse dorsal osteoderm rows are thus associated with the anterior of the two vertebrae they overlap.

Huxley (1859) restricted his observations to the scutes on the body and anterior part of the tail, and Seidel (1979) noted that an interruption in the series of dorsal median arteries occurred in the shoulder region, although it continued anterior to this. Gadow (1901) also noted the difference between trunk and cervical armor in the Crocodilia, stating that, "the armor of the recent forms consists, so far as the large scutes are concerned, of a considerable number of scutes, which are arranged in transverse rows, each row corresponding with one skeletal segment of the trunk proper. Mostly there is a detached cluster of scutes on the neck." Indeed, there is sometimes a detached cluster of scutes on the neck, particularly in *Crocodylus*, but other forms (e.g., *Gavialis*, *Tomistoma*, *Melanosuchus*) possess continuous thoracic and cervical armor.

As illustrated in Figures 1 and 2, radiographs and dissection show the one-to-one relation between vertebrae and dorsal armor, and that in certain cases some scutes on the neck overlap two vertebrae. Dissection confirms Huxley's observation of association between neural spines and osteoderms. There are normally 26 precaudal vertebrae (24 presacral + 2 sacral) plus a proatlas in all living and fossil forms examined. For further discussion of vertebral morphology, see Higgins (1923), Hoffstetter and Gasc (1969), and Romer (1956).

MATERIALS AND METHODS

Our taxonomy of the living Crocodilia follows Wermuth and Mertens (1961) at the generic and specific level. We do not consider subspecies. We have followed Boulenger (1889) in ordering the genera as follows: *Gavialis*, *Tomistoma*, *Crocodylus*, *Osteolaemus*, and finally *Alligator* and the caimans.

Determinations were made on the basis of cranial characters, coloration, and geographic provenance. We examined skins, mounted, and fluid preserved specimens of all living species. The Appendix is a list of specimens examined and reported on in this paper. In addition, we incorporate some data from the

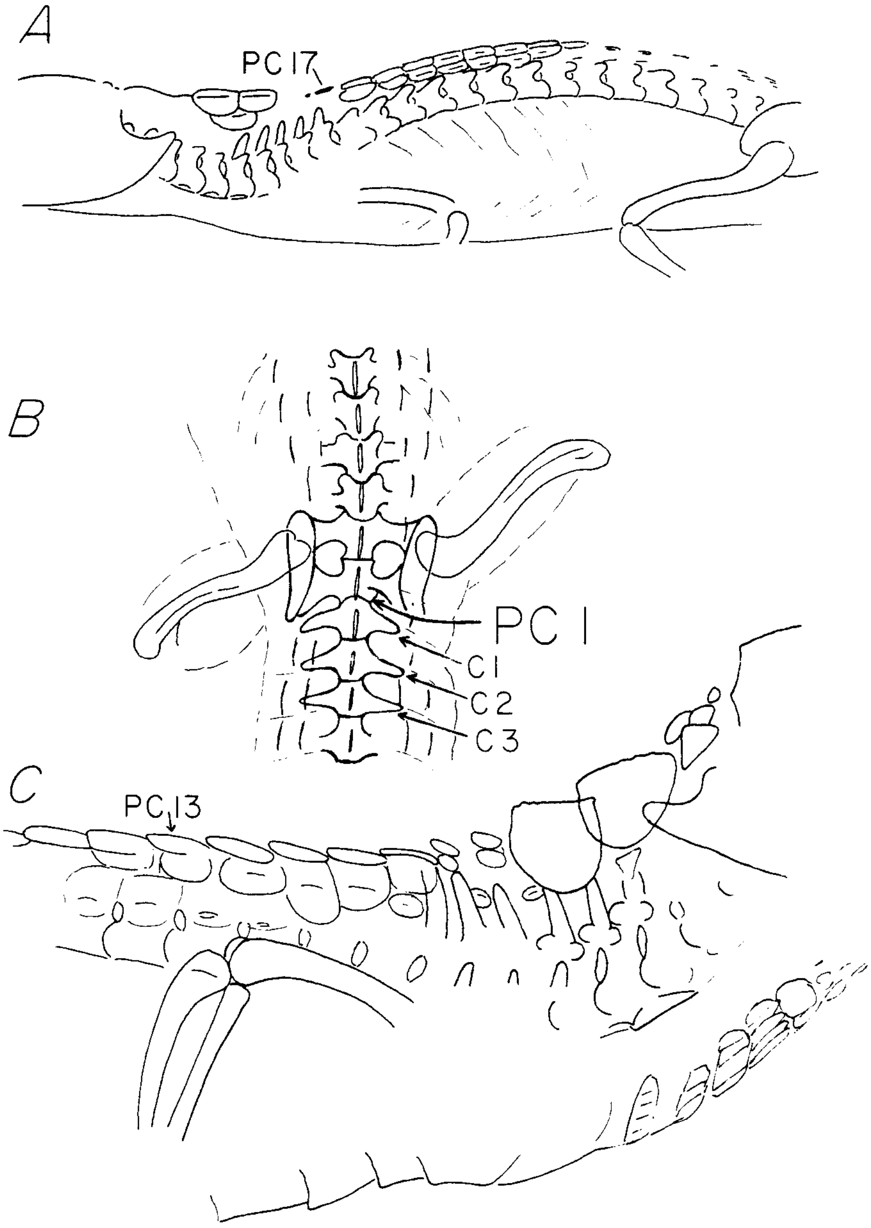

Figure 1. Tracings of radiographs showing endo-and exoskeletal systems in: A. *Crocodylus siamensis*, MCZ 3716, lateral view of the neck and trunk region. B. *Osteolaemus tetraspis*, MCZ 3589, dorsal view of the lumbar, sacral, and anteriormost caudal regions. C. *Osteolaemus tetraspis*, MCZ 2017, lateral view of the anterior thoracic and all of the cervical series.

literature; and, in the case of *Crocodylus intermedius*, we have relied in part on photographs and a personal communication regarding the type. The type of *Protosuchus richardsoni* (AMNH 3024) was also examined.

Specimens of *Osteolaemus tetraspis, Tomistoma schlegelii, Melanosuchus niger, Paleosuchus trigonatus, P. palpebrosus, Caiman crocodilus, C. latirostris, Alligator sinensis, A. mississippiensis*, and nine species of *Crocodylus* were radiographed to determine the relationship between the dorsal armor and the skeleton, and for vertebral counts. Additional vertebral counts were performed on skeletons.

METHODOLOGY

Although the tradition has been to count both dorsal armor and vertebrae from the cranium, we count away from the sacro-caudal juncture in both precaudal (PC) and caudal (C) series (Figs. 2, 4). PC 1, the posteriormost transverse precaudal scale row, hangs posteriorly from the tip of the neural spine of the posterior sacral vertebra. PC 1 can be identified unambiguously in fluid preserved specimens by a simple dissection. An incision is made along the medial, posterior, and lateral borders of three transverse rows on one side of the body: the two rows nearest the posterior edge of the iliac crest and the one anterior to them. The skin and osteoderms are then reflected anteriorly, and the musculature dorsal to the level of the sacral ribs removed, thus revealing the relationship between the vertebrae and the osteoderm rows. PC 1 is the transverse row extending posteriorly from the neural spine of the posterior sacral, and dorsal to the postzygapophysis of the same vertebra. The reflected skin and osteoderms may be folded back, leaving the specimen externally unchanged, and the musculature of the other side of the body intact for anatomical studies. Radiographs from dorsal view also allow unambiguous identification of PC 1, provided the osteoderms are sufficiently opaque to X-rays (Fig. 1B).

Short of dissection or X-ray, the following criteria have been found useful in the identification of PC 1. First, PC 1 lies between the posterior blades of the ilia. The posterior edge of the iliac blades are overlain by PC 1 or the anterior portion of the first caudal row (C 1). The location of the blades can be determined by palpation. Secondly, when held perpendicular to the body, the long axis of the femurs passes through PC 2 or the border between PC 2 and PC 1. Third, in many species, PC 1 is the first transverse row to become broader after monotonically decreasing in breadth from midbody towards the sacrum (see Figs. 2B, 3C). Finally, the posterior edge of PC 1 is often at the posterior edge of the hind limb (the traditional point of demarcation between dorsals and caudals), but this is not always the case. When these criteria are applied simultaneously, PC 1 can usually be identified unambiguously. Reference to radiographs and dissected specimens is always helpful. PC 1 has been identified by these criteria in most specimens examined in this study.

Skins and stuffed specimens present special problems. Determination of the relationship of the transverse rows to the variously granulated scales around the base of the hind limb in intact specimens, and criterion three above are the best guides to the identification of PC 1 in such specimens. Comparison with intact specimens is helpful.

Posterior to PC 1, the caudal series consists first of double crest caudals and then single crest caudals. Double crest caudals are associated with vertebrae with transverse processes, and have two to four keels across. Single crest caudals are associated with vertebrae having reduced or absent transverse processes, and have a single median keel. The keel of the single crest series and the outer keels of the posterior double crest series form a Y-shaped swimming keel.

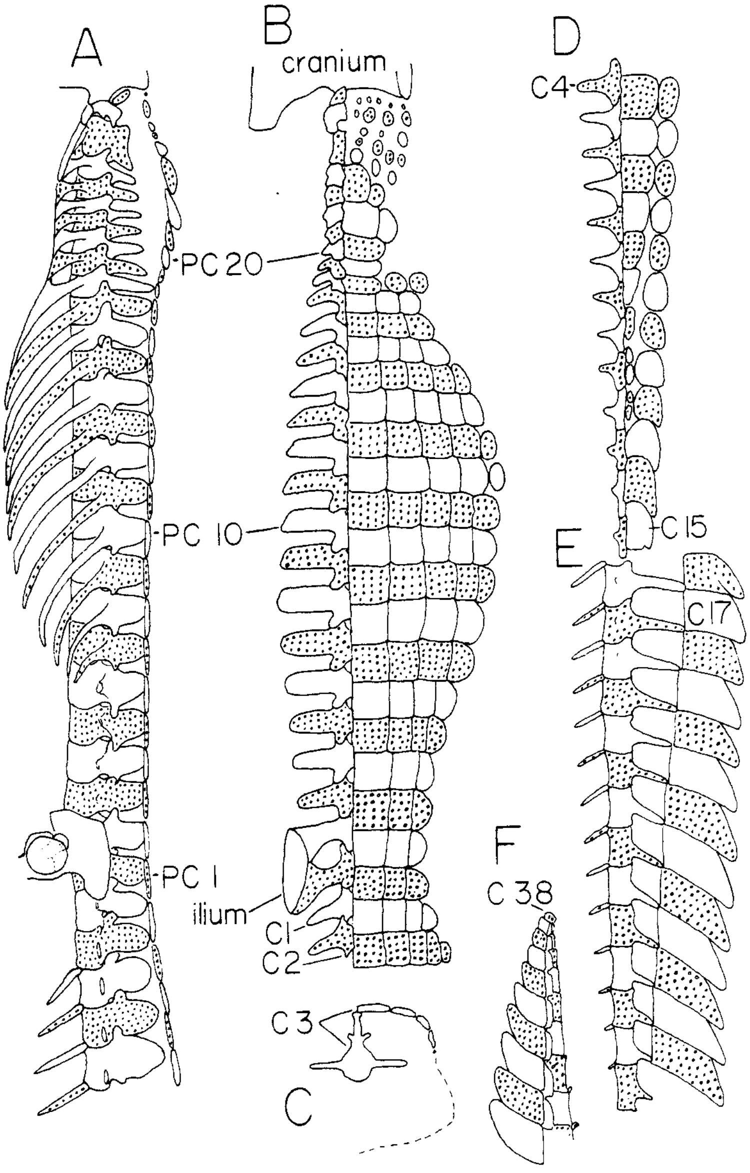

Figure 2. Semidiagramatic illustration of the one-to-one relationship between vertebrae and transverse rows of dorsal osteoderms as revealed by dissection of *Melanosuchus niger*, MCZ 17726. Odd numbered elements stippled in the precaudal (PC) series, and even numbered elements stippled in the caudal (C) series. A. PC 26-C 5 in lateral view. B. PC 26-C 2 in dorsal view. C. C 3 in cross section. D. C 4-C 15 in dorsal view. E. C 16-C 28 in lateral view. F. C 29-C 38 in lateral view.

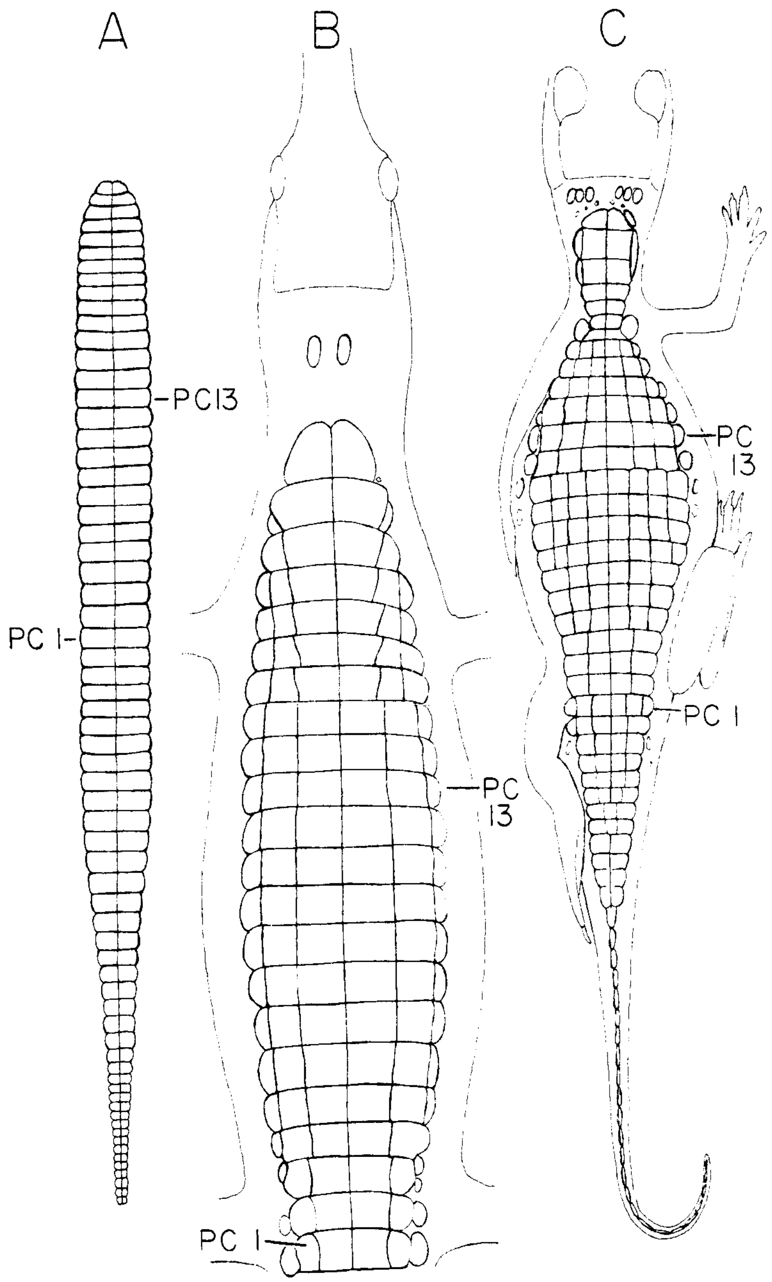

Figure 3. Dorsal armor of three selected crocodilians. A. *Protosuchus richardsoni*, AMNH 3024, type, after Colbert and Mook, 1951 (PC 27-C 39 shown). B. *Gavialis gangeticus*, BMS no #, from the head to the sacro-caudal juncture; C: *Caiman crocodilus*, MCZ 3394, full body.

On the lateral and ventral surfaces of the base of the tail, scales may occur in various configurations which break up the regular (in the sense of showing plane symmetry; see Breder, 1947) disposition of scales in this area. These are collectively termed basicaudal irregularities. Four kinds are recognized: 1) a thin horizontal strip of granular skin separating the dorsal from the lateral scalation; 2) one or more thick strips of granular skin on the dorsolateral surface (Fig. 11); 3) lateral intrusions, in the form of small vertical arrays of scales, two-thirds or more of a normal scale in height, on the postcloacal lateral surface, sometimes present on one side only (Fig. 4; Ross and Ross, 1974: Fig. 1a); and 4) large ventrolateral intrusions composed of vertical arrays of scales on the postcloacal ventral and ventrolateral surfaces (Fig. 4; Ross and Ross, 1974: Fig. 1b). This last increases the number of midventral transverse rows relative to the dorsals.

Anterior to and including PC 1 is the continuous and contiguous precaudal armor (Fig. 4). The *continuous* armor is the series of transverse rows beginning with PC 1 and extending to the row which is bordered in front by a missing transverse row. Soft skin may intrude between two rows without a row being absent. This makes the armor appear discontinuous, although all rows are present. The *Crocodylus moreletii* in Fig. 4 has 16 continuous precaudal rows, PC 17 (and others) being absent. *Contiguous* scutes are scutes in a series crossing (or at least touching) the midline in which adjacent members of the series are in contact. Beginning with PC 1, the number of contiguous scutes per transverse row in Figure 4 is 4, 4, 4, 4, 6, 4, 4, 4, 6, 3, 3, 6, 5, 2, 4, 2.

Additional characteristics of the trunk armor are the presence of detached lateral scutes, sometimes forming a longitudinal row (Fig. 4), the alignment and extent of development of keels on the scutes, the uniformity of scute size, and the presence of left/right asymmetries. Note that even development and alignment of keels, uniformity of scute size, and absence of asymmetry impart the quality of "regularity" to the armor.

The cervical shield is the cluster of scutes on the neck. The term does not refer to particular precaudal rows, as the rows comprising it and its continuity with the thoracic armor vary among species. The nape region is the area between the occiput and the cervical shield. Vertebral correspondence in the cervical region is determined in two ways. In species with a continuous thoracic and cervical armor, correspondence can be determined directly by counting, with observation of individual variation revealing compound rows. In species with discontinuous cervical and thoracic armor, comparison with related species is necessary. For example, in *Crocodylus* all species have two enlarged rows in the cervical shield. In *C. cataphractus* (Fig. 5D), and frequently in *C. johnstoni* (Fig. 6A), the cervical and thoracic armor is continuous, the last row before the two enlarged rows being PC 19. Thus the enlarged rows begin with PC 20. Individual variation in *C. niloticus* (Fig. 6B-D) shows that these enlarged rows are each compound. Assuming that these rows are homologous among members of the genus allows extrapolation to other species. Thus the *C. moreletii* in Fig. 4 has two scutes in PC 20 + 21 and four in PC 22 + 23. Uncertain homologies might be resolved by careful dissection of arteries and nerves.

Analysis of the cervical region requires comparison of many specimens simultaneously. We found photographs useful in comparing specimens from different institutions. A marker with specimen number was placed on PC 12, and both marker and PC 13 forward photographed from directly above. Properly marked photographs proved to be as good as actual specimens for comparative purposes. We would encourage the collection of photographs of this kind, as it allows obtaining sizable samples without damaging populations of the world's

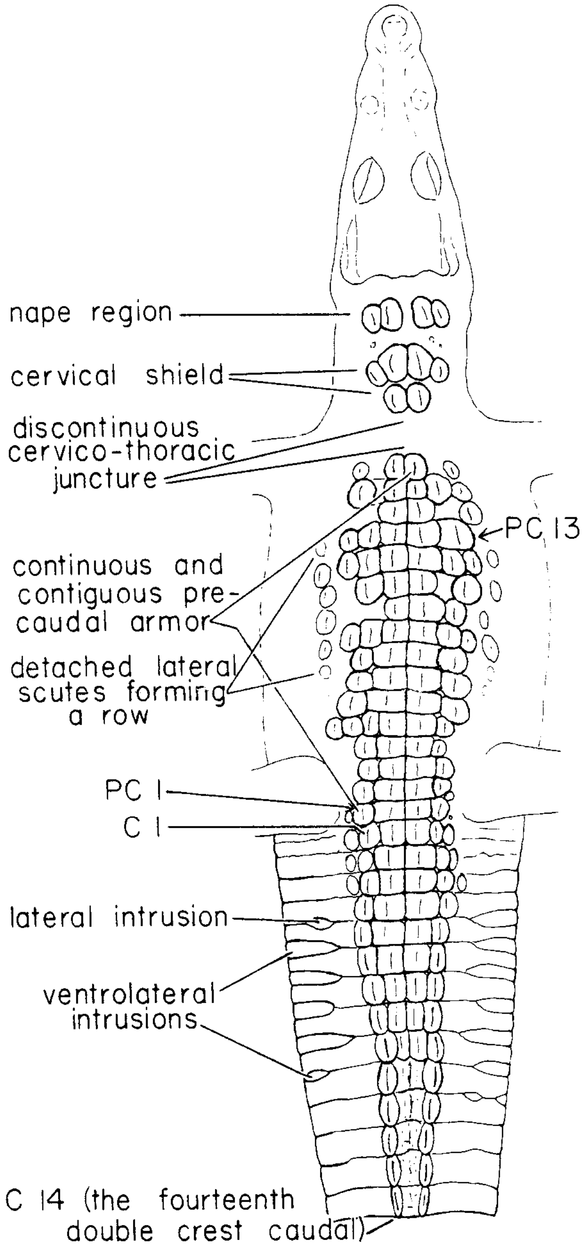

Figure 4. Some terms used in this paper indicated on *Crocodylus moreletii*, USNM 71955, topotype. From an original drawing by Aleta Karstad.

dwindling supply of crocodilians. The photographs can be stored as a record of the specimens examined in natural populations without removing individuals from those populations.

Meristic characters in reptiles are generally believed not to change in postembryonic life (Hecht, 1952; Kerfoot, 1970; Fox, 1975). Our observations support this. Although we have not studied large series, examination of embryos of various ages from a variety of species indicates that there is little or no ontogenetic change in embryonic life as well. The scutes of unpigmented embryos are somewhat more closely spaced, and thus may appear contiguous or continuous, whereas in hatchlings and adults they would not be in contact. Thus available ontogenetic data does not help to elucidate homology of transverse rows. Medem (1958a) noted that *Crocodylus intermedius* embryos did not differ from adults in scale counts.

There are two exceptions to the general rule of no ontogenetic change. First, the number of single crest caudals decreases due to injury and wear on the tail. Counts of this character are thus possible only on undamaged individuals. Second, and more interesting, the number of scutes per transverse row in *Gavialis* decreases from six to four as an animal ages. This is discussed in the species accounts. Deraniyagala (1939) also noted some ontogenetic changes in *Crocodylus porosus* embryos, involving a decrease in the number of small scales interspersed among the scutes of the trunk armor.

SPECIES ACCOUNTS

The following accounts of the species provide brief descriptions of the dorsal armor of each species, with more detailed treatment of the anterior region, where the greatest variation within and among species occurs. Table 1 gives counts of the contiguous scutes per transverse row for PC 1 to PC 18 for all species. In Table 2, the number of double and single crest caudals is given for each species. All living crocodilians have a Y-shaped caudal swimming keel, consisting of the single crest caudals and the posterior part of the double crest series. The ways in which the Y-shaped keel is formed from the keel rows of the trunk armor as it passes over the pelvis in different taxa are given in Table 3. Table 4 records the occurrence of basicaudal irregularities.

Gavialis gangeticus

In *Gavialis* (Fig. 3B), the continuous and contiguous precaudal armor is remarkably uniform in scute size and shape, and keel row alignment and development. There are six scutes per transverse row in PC 1 to PC 18 in hatchlings and young. In older specimens, there are only four scutes across, apparently because the lateral D-shaped scales of the very young fail to ossify with the four more medial scutes. This is unique in the Crocodilia. There are no detached lateral scutes on the flanks, and the thoracic and cervical armor are continuous. There are 22 continuous rows of precaudal armor, narrowing anteriorly to two scutes in PC 22. The nape is naked except for two prominent scutes and occasional traces of others.

Tomistoma schlegelii

In *Tomistoma* (Fig. 5A-C), the continuous and contiguous precaudal armor is quite regular, with five to eight, usually six, scutes across at midbody (PC 9-PC 12). Detached lateral elements form an additional row on each flank. The thoracic and cervical armor are continuous forward to PC 23, and narrowest at PC 19 or PC 20. There are two scutes in PC 18, 19, 20, and 21. Typically, the terminal row is PC 22+23 compound with two elements. In some specimens PC 23 is present as a distinct row or asymmetrically. Fig. 5A-C shows the range of variation in this region. Scutes on the nape are ir-

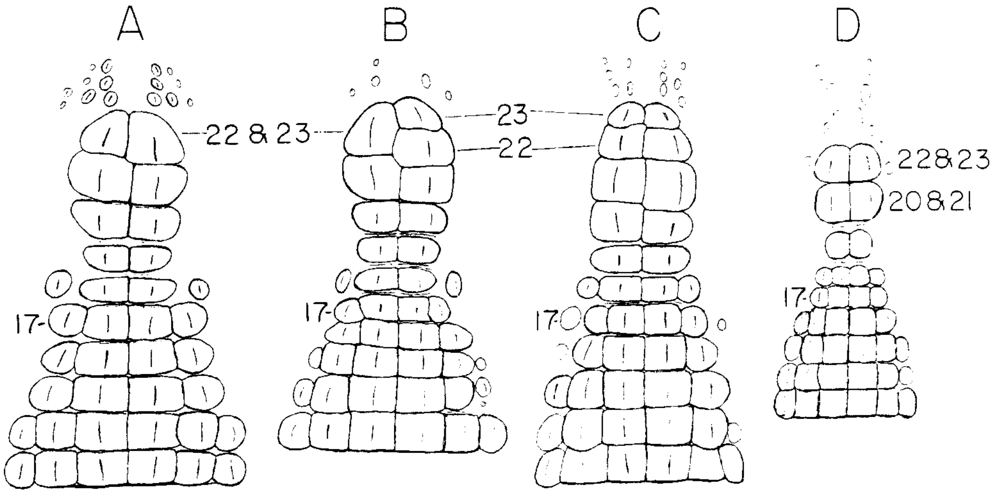

Figure 5. Anterior end of the dorsal armor, PC 13 forward, with selected scale rows numbered. A. *Tomistoma schlegelii* FMNH 206755. B. *T. schlegelii*, USNM 145587. C. *T. schlegelii*, USNM 58136; D. *Crocodylus cataphractus*, MCZ 54650.

regularly placed, although sometimes appearing as three transverse rows, presumably PC 24 to PC 26. This latter condition is clearly seen in Figure 5A.

Crocodylus cataphractus

In *Crocodylus cataphractus* (Fig. 5D), the continuous and contiguous precaudal armor is regular in scute size and keel row alignment. There are four to eight, usually six, scutes across at midbody. The median scute pair of each row tends to be broader than the laterals and have lower keels. Detached lateral elements are present and sometimes form an additional keeled row on each side. PC 19 is bordered front and back by short spaces of soft skin. PC 20 + 21 and PC 22 + 23 are compound rows of two elements each. The compound nature of these rows is demonstrated in other species of *Crocodylus*. The nape rows are variably developed, but for the most part are vestigial. The largest elements appear to be from PC 26.

Crocodylus johnstoni

In *Crocodylus johnstoni* (Fig. 6A), the continuous and contiguous precaudal armor is regular and has six to seven, usually six, scutes across at midbody. Detached lateral scutes form one or two additional well-developed keeled rows on each flank. The thoracic and cervical armor are continuous, but small spaces of soft skin occur between the transverse rows at the cervico-thoracic juncture. Sometimes there is but a single scute in PC 18 or PC 19 (Fig. 6A). PC 20+21 has two large scutes, and PC 22+23 has four, for a total of six fairly closely juxtaposed scutes forming an ovate shield. The two lateral elements of PC 22+23 are often displaced posteriorly, their medial edge bordering the juncture between PC 20+21 and PC 22+23. The nape has

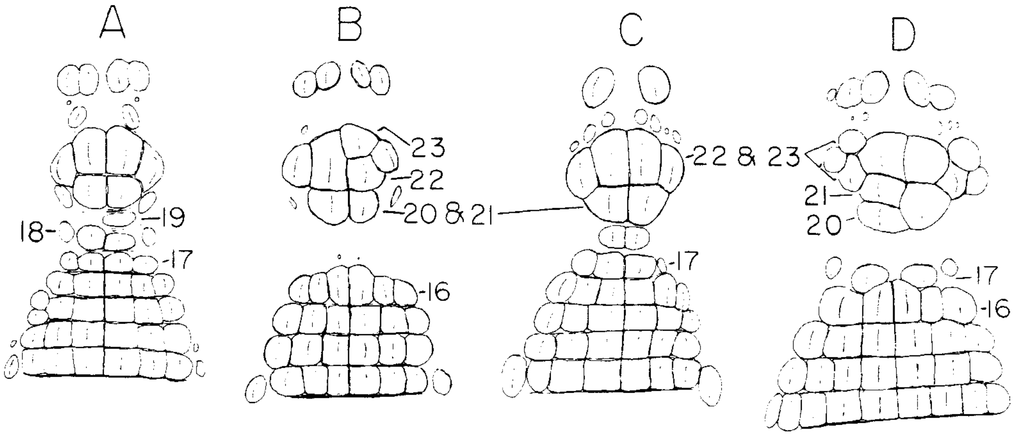

Figure 6. Anterior end of the dorsal armor, PC 13 forward, with selected precaudal scale rows numbered on: A. *Crocodylus johnstoni*, MCZ 35006. B. *C. niloticus*, USNM 195783. C. *C. niloticus*, MCZ 12552. D. *C. niloticus*, USNM 63592.

three to six scutes in PC 26. PC 25 appears lost or perhaps coalesced with PC 26. PC 24 has zero to four minor elements.

Crocodylus niloticus

In *Crocodylus niloticus* (Fig. 6B-D) the continuous and contiguous precaudal armor is moderately regular, particularly in the sacral and lumbar regions and along the midline. There are 16 or 17 continuous rows of precaudal armor, with four to nine, usually six, scutes per transverse row at midbody. The median scute pair of the anteriormost thoracic row is often enlarged. Laterally, detached elements may form up to two additional keeled rows. In some individuals, especially from Madagascar, a row of two scutes intervenes between the thoracic and cervical armor. We interpret this as PC 19 on the basis of it being closer to the cervical than the thoracic armor, but this identification is not certain. PC 20+21 has two scutes, and PC 22+23 has four. These two transverse compounds tend to be closely adjacent, forming an ovate cervical shield. The compound nature of these rows is demonstrated by occasional variants exhibiting one or the other row in an uncompound state (Fig. 6B, D). The nape has three to six scutes in PC 26, and zero to four small elements in PC 24. PC 25 is absent, or perhaps fused with PC 26.

Crocodylus palustris

In *Crocodylus palustris* (Fig. 7D), the continuous and contiguous precaudal armor is fairly regular. At the anterior end of the thoracic armor, small scales sometimes occur between transverse rows and between the scutes within a transverse row, leading to a loss of contiguity. There are four to eight contiguous scutes per transverse row at midbody, with no outstanding modal number. Detached lateral scutes form one or two additional keeled rows, the more medial particularly well developed. The thoracic and cervical armor are distinctly separated by a space of granular skin. PC 17 has zero to four scutes, and vestiges of PC 18 are rarely present. PC 19 is absent. PC 20+21 has two scutes, and PC 22+23 has four. Sometimes an additional pair of scutes is in contact laterally, giving a total

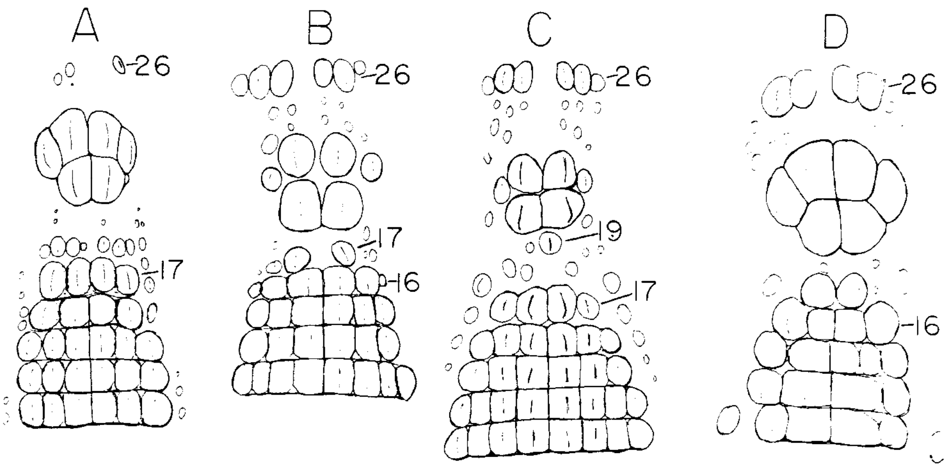

Figure 7. Anterior end of the dorsal armor, PC 13 forward, with selected precaudal scale rows numbered on: A. *Crocodylus porosus*, USNM 72732. B. *C. novaeguineae*, from New Guinea, CAS 119186. C. *C. novaeguineae*, from the Philippines, FMNH 52362. D. *C. palustris*, FMNH 63739.

of eight scutes in the cervical shield. Traces of PC 24 are sometimes evident. PC 25 is absent or perhaps combined with the normally four scutes in PC 26.

Crocodylus siamensis

In *Crocodylus siamensis* (Fig. 8A), the continuous and contiguous precaudal armor is regular, though often with small triangular scales interspersed between the scutes along the posterior border of a transverse row, as is also found in *C. porosus*. There are four to seven, usually six, scutes across at midbody. Detached scutes form one or two additional rows on the flanks. PC 18 is usually absent, and PC 19 always is. There is a cervical shield of two scutes in PC 20+21 and four scutes in PC 22+23, and sometimes remnants of PC 24. PC 25 is absent or perhaps combined with the two to usually four scutes in PC 26. *C. siamensis* is reported to hybridize with *C. porosus* in captivity, producing phenotypically intermediate and allegedly heterotic offspring (Youngprapakorn, 1976). The fertility of the hybrids is not reported.

Crocodylus porosus

In *Crocodylus porosus* (Fig. 7A), the continuous and contiguous precaudal armor is regular in keel row alignment and with six to eight, usually six, narrow elements per transverse row at midbody. Small triangular scales occur interspersed between scutes along the posterior edges of transverse rows. Anteriorly, these small elements also occur along the anterior borders of scute rows, and may contact the posterior triangles, breaking contiguity. Lateral detached scutes are quite small and indistinct. The thoracic and cervical armor are completely discontinuous. PC 17 is usually absent. PC 18 is sometimes represented by vestiges. PC 19 is absent entirely. PC 20 + 21 has two scutes, and PC 22 + 23 has four. The nape is essentially naked. In specimens examined by us PC 24 to PC 26 are usually absent, though rarely two distinct

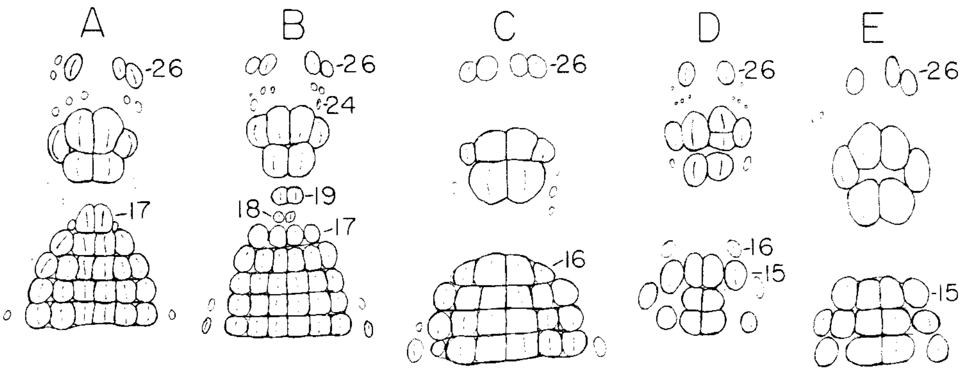

Figure 8. Anterior end of the dorsal armor, PC 13 forward, with selected precaudal scale rows numbered on: A. *Crocodylus siamensis*, MCZ 3716. B. *C. rhombifer*, MCZ 12081. C. *C. intermedius*, FMNH 75658. D. *C. acutus*, FMNH 23147. E. *C. acutus*, MCZ 10920.

scutes may occur in PC 26. Deraniyagala (1939) reports specimens with up to four.

Crocodylus novaeguineae

In *Crocodylus novaeguineae* (Fig. 7B, C), the continuous and contiguous precaudal armor is regular in scute dimensions and keel row alignment. As in *C. porosus* and *C. siamensis*, interscute triangles occur. There are 16 or 17 continuous precaudal rows, with seven to twelve, usually eight, contiguous scutes at midbody. Detached flank scutes, though reduced, sometimes form an additional keeled row on each side. The thoracic and cervical armors are separated by spaces of skin. PC 18 is represented by vestiges or elements separated on the midline. PC 19 is absent, or, in a single specimen, rudimentary. PC 20+21 has two scutes, and PC 22+23 has two large median elements, and may have one or two smaller elements on either side. In many individuals, smooth or fine granular skin separates the two cervical rows (PC 20+21 and PC 22+23) or the left and right halves of one or both (Fig. 7B). Sometimes PC 22 and PC 23 are not compound. All or any combination of cervical scutes may be noncontiguous. There are four to six scutes in PC 26. PC 24 and PC 25 are sometimes not evident, but are usually present as bluntly keeled scales.

Previous authors have differed on whether the freshwater crocodiles of the Philippines should be recognized as a species (*mindorensis*) distinct from *C. novaeguineae*, or merely as a subspecies of the latter (Wermuth, 1953; Schmidt, 1956; Wermuth and Mertens, 1961). Wermuth and Mertens, in their most recent checklist (1977), have elevated *mindorensis* to full species status. Tables 1 and 2 include with *C. novaeguineae* data for a few *mindorensis*. The preceding account of the cervical armor, however, applies only to *C. novaeguineae* proper. *C. mindorensis* (Fig. 7C) differs from *C. novaeguineae* in that PC 19 is better developed, being present as one or two elements in three of five individuals; PC 22+23 has four elements; the scutes of the cervical shield are little or not at all separated by skin; and the nape scutes between the cervical shield and the prominent nape row (PC 26) are better developed, sometimes in two distinct rows. The extremal count of twelve scutes at midbody is from an individual from the Philippines. In general, *mindorensis* has a more well-developed armor than *novaeguineae*, though this conclusion is based on a small sample and should be considered tentative.

Crocodylus rhombifer

In *Crocodylus rhombifer* (Fig. 8B), the continuous and contiguous precaudal armor is often remarkably even and regular. There are six or seven, usually six, scutes across at midbody, and detached lateral elements form one or two additional keeled rows. Some individuals have continuous cervical and thoracic armor, others do not. PC 18 has one or two scutes. Sometimes there is a space of soft skin between PC 18 and PC 19, and invariably between PC 19 and PC 20+21. PC 19 is variously absent or present as two scutes. PC 20+21 has two scutes and PC 22+23 has four. Anterior to the cervical shield, scutes are poorly developed, except for a row of four prominent scutes, presumably PC 26. *C. rhombifer* is easily distinguished from *C. acutus* by having six or more scutes in all four transverse rows at midbody. The two species are reported to hybridize in the wild and in semi-captivity (Varona, 1966; Anonymous, 1969). A presumptive wild hybrid, AMNH 82943, has the black and white flecked coloration of *C. rhombifer*, and regularity of the dorsal armor like *rhombifer*, but has fewer contiguous scutes at midbody than *rhombifer*, is lacking PC 17 entirely, and has a head with *C. acutus* proportions and snout character.

Crocodylus moreletii

In *Crocodylus moreletii* (Fig. 4), the continuous and contiguous precaudal armor is fairly irregular and asymmetric, with the contiguous scutes at midbody often reduced to three or four. There are two to six, usually four, contiguous scutes across at midbody, and detached elements on the flank are always present. PC 17 and PC 18 are absent, and PC 19 has zero to two scutes. PC 20+21 has two scutes, and PC 22+23 usually has four. PC 24 is variably developed, sometimes absent. PC 25 is absent or perhaps compounded with the four to six scutes in PC 26.

Natural hybrids have been reported between *Paleosuchus trigonatus* and *P. palpebrosus* (Medem, 1970) and *Crocodylus rhombifer* and *C. acutus*. In both cases, the presumed hybrids closely resembled one of the parent species, though possessing certain minor, yet characteristic, traits of the other parent. It is probable that hybridization has also occurred between *C. acutus* and *C. moreletii*. Ross and Ross (1974) used a combination of several cranial characters and body color to identify *C. acutus* from throughout its range, and found traces of a *C. moreletii* character (lateral intrusions on the basicaudal surface; see Fig. 4) on *C. acutus* only where they are sympatric with *C. moreletii* (Belize through Chiapas), or where the population could have been influenced by hybrid stock (west coast of Mexico; it is interesting that fossil *C. moreletii* have been reported from Baja [Miller, 1980]). The dorsal armor of presumptive hybrids resembles both parent species in scale counts, but in this case both parent species have remarkably similar dorsal armor.

Crocodylus acutus

In *Crocodylus acutus* (Fig. 8D, E), the continuous and contiguous precaudal armor is highly irregular in scute size, scute shape, and disposition. The median scute pairs of each row are fairly even in length, except anteriorly, where midline irregularities and gross asymmetry may occur. There are two to six, usually four, scutes across at midbody, always with asymmetry in at least some rows. There are always detached scutes on the flank. There are 14 to 17, usually 16, continuous precaudal rows. There is a tendency for the anteriormost median scute pair of the continuous armor to be large and flanked by noncontiguous elements. PC 18 is always absent. PC 19 is almost always absent. PC 20 – 21 has two elements, and PC 22 + 23 has four, forming a cervical shield of six elements, though variations by deletion are common. PC 24 is vestigial, or more often absent, and PC 25 is absent or perhaps fused with the two to four elements of PC 26.

Crocodylus intermedius

In *Crocodylus intermedius* (Fig. 8C), the continuous and contiguous precaudal armor is more or less regular in scute dimensions and keel row alignment. There are five or six contiguous scutes per transverse row at midbody, with a variable development of detached flank scutes sometimes forming an additional keeled row. There are 16 continuous precaudal rows. One of our specimens has a "normal" *Crocodylus* cervical shield and nape region: PC 20+21 with two elements, PC 22+23 with four elements, and PC 26 with four. Our other specimen has three transverse rows in the cervical shield, with two scutes in each of the two posteriormost, and four in the anteriormost. The nape is "normal" with five scutes. Our sample of *C. intermedius* is small, consisting of a single museum specimen, and photographs of a living individual in the collection of F. Medem. C. A. Ross (personal communication) describes the type (MNHN Paris 7512) as having heavy thoracic armor of six, sometimes even seven contiguous scutes across. There are no detached lateral scutes. The neck has six scutes in a shield, and there are five scutes in the nape row.

Osteolaemus tetraspis

In *Osteolaemus tetraspis* (Fig. 9A), the continuous and contiguous precaudal armor is more or less regular, the median scute pairs the broadest, and with keels poorly developed or lacking. There are four to eight, usually six, scutes per transverse row at midbody, and detached scutes on the flanks. PC 18 usually consists of two elements contiguous on the midline, often with detached lateral elements with very small, vestigial scales between them. Anterior to PC 18 there is a fold of skin, a row of two small elements, another fold of skin, and then two rows of two large elements each. The anteriormost of these large rows is usually the longest of the two. In a single specimen (Fig. 9A), only one row of two small elements occurs between PC 17 and the two large rows of the cervical shield. There is usually one well-developed row of four scutes on the nape. Some specimens show an additional pair of scutes. Radiographs (Fig. 1C) show that the large neck scutes overlie vertebrae PC 21 and PC 22, and PC 23 and PC 24. However, vertebral correspondences of all cervical scutes and the nape are uncertain.

Alligator sinensis

In *Alligator sinensis* (Fig. 9C), the continuous and contiguous precaudal armor has six to eight, usually six, scutes at midbody, and few or no lateral detached scutes on the flanks. The thoracic and cervical armors are separated by at least a small space of skin. PC 17 is sometimes absent, but usually present with up to five elements. PC 18 is usually absent. Anterior to this there is a strip of skin followed by three transverse rows of two scutes each. The size of these scutes increases anteriorly. The nape has a row of four to six prominent scutes, and sometimes an additional row of two between the prominent row and the cervical shield. The vertebral correspondences of the cervical shield and the nape are uncertain due to the discontinuity at the cervico-thoracic juncture and the relatively slight variation among individuals. The prominent nape row is likely PC 25, as it is in *A. mississippiensis*, leaving PC

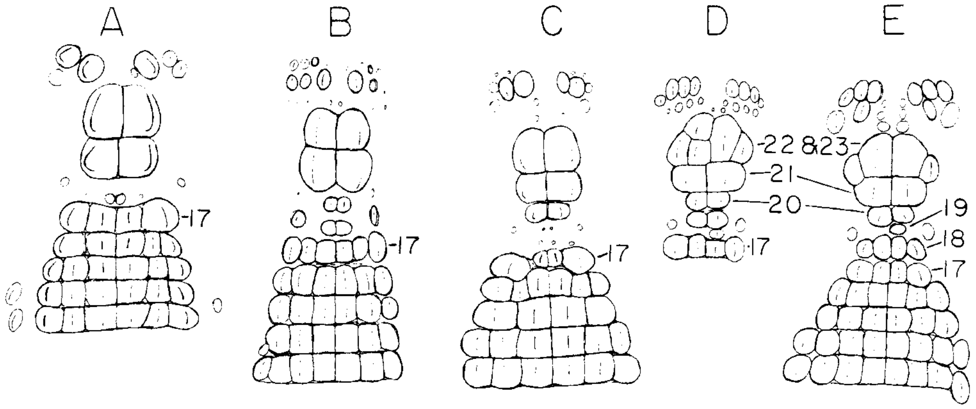

Figure 9. Anterior end of the dorsal armor, with selected precaudal scale rows numbered, PC 13 forward on: A. *Osteolaemus tetraspis*, USNM 193289. B. *Alligator mississippiensis*, MCZ 17723. C. *A. sinensis*, FMNH 38234. PC 17 forward on: D. *Caiman crocodilus*, MCZ 15334. PC 13 forward on: E. *C. latirostris*, MCZ 3588.

19 to PC 24 to be accounted for by the three rows of the cervical shield and the smaller nape row. The possibility of compounding is indicated by the large size of the anteriormost of the three rows of the cervical shield.

Alligator mississippiensis

In *Alligator mississippiensis* (Fig. 9B), the continuous and contiguous precaudal armor is five to eight, usually eight, scutes across at midbody, and there are no detached scutes on the flanks. The thoracic and cervical armors are barely continuous, having reduced elements in PC 18 to PC 19, and possibly PC 20, and two folds of skin in the cervico-thoracic juncture. PC 18 is ordinarily present as two small scutes. There are ordinarily lateral scutes which may be from PC 18 or traces of PC 19 (we don't know which). If PC 19 is absent on the midline, there are two scutes in PC 20, two very long elements in PC 21+22, two in PC 23, and then the nape scales. If the posteriormost neck scute is PC 19, PC 20+21 has two very long scutes, and PC 22+23 has two shorter scutes, and then there are the nape scutes in two or three rows separated on the midline. The most prominent nape row is PC 25, ordinarily with two, but with up to six ossified elements. PC 25 is the postoccipital of Ross and Roberts (1979); in *Crocodylus* this term refers to PC 26.

Caiman latirostris

In *Caiman latirostris* (Fig. 9E) the continuous and contiguous precaudal armor varies from regular to somewhat irregular in the alignment of the keels. There are six to nine, usually six, scutes across at midbody, with detached lateral scutes tending to form additional rows on the flanks. The thoracic and cervical armor are usually discontinuous. PC 18 has two to four elements. PC 19 is normally absent, but may be present in rudimentary fashion (Fig. 9E). There are three transverse rows anterior to PC 19 (or PC 18 when PC 19 is absent) in the cervical shield, with two scutes in the two posteriormost, and four in the anteriormost row. The vertebral correspondences of these rows are uncertain, but are probably PC 20, PC 21, and PC 22+23 compound. In a single specimen (MCZ 17716), PC 24 is well developed and continuous with the cervical shield. The nape consists usually of PC 24 to PC 26, with PC 26 most strongly developed.

Caiman crocodilus

In *Caiman crocodilus* (Figs. 3C, 9D) the continuous and contiguous precaudal armor tends to have low keels in longitudinal alignment, and the detached scutes on the flanks tend to be aligned in additional rows. There are six to twelve, usually eight, scutes across at midbody. The thoracic and cervical armors are sometimes not truly continuous, though they appear so with only narrow strips of skin where PC 18 or PC 19 are lost. There are usually four scutes across somewhere in the PC 21 to PC 23 region, often in PC 23. PC 24 is variously absent, vestigial, or present and rarely (Fig. 3C) continuous with the cervical shield and contiguous across the midline. The nape appears to be PC 24 to PC 26, sometimes PC 25 to PC 26 only. Some specimens exhibit 26 transverse precaudal rows without loss or compounding, but about half of the specimens examined show left-right asymmetry and fewer than 26 transverse precaudal rows. In these specimens it is difficult to determine which rows have been lost or fused. Figure 9D is a probable interpretation.

Melanosuchus niger

In *Melanosuchus niger* (Fig. 2) the continuous and contiguous precaudal armor is regular, with nine to twelve, usually ten scutes across at midbody, and there are no detached lateral scutes. There are four to six scutes in PC 18, two to four in PC 19, two to four in PC 20, two to four in PC 21, and four in PC 22 and PC 23. Remnants of PC 24 to PC 26 in approximately three transverse rows give the nape an overall granular and studded appearance. There are invariably 23 continuous precaudal rows in our sample.

Paleosuchus palpebrosus

In *Paleosuchus palpebrosus* (Fig. 10D) the thoracic armor is broad with more or less regular keel row alignment and scute dimensions. There are four scutes in PC 2 to PC 5, and six to nine, usually eight, contiguous scutes at midbody. The precaudal armor is continuous to PC 18. PC 18 has three to six elements. PC 19 is often bordered anteriorly and posteriorly by soft skin, and is reduced in size. There are two contiguous elements in PC 19, PC 20, PC 23, and PC 24. PC 21 and PC 22 may have four or, usually, three elements. PC 24 may be continuous with or separated from the cervical shield. PC 25, as here interpreted, consists of lateral elements and, in one specimen (Fig. 10D), a single element adjacent to the midline. The most prominent row on the nape is PC 26 with four to six elements. *P. palpebrosus* is much more ossified than its congener. This is seen in the greater breadth of its dorsal armor, the continuity between the thoracic and cervical armor, and the greater ossification of the skull and the ventral armor (Medem, 1958b).

Paleosuchus trigonatus

In *Paleosuchus trigonatus* (Fig. 10A-C) the dorsal armor is four to eight, usually six, scutes wide at midbody and often highly irregular in keel row alignment and scute size and shape. These irregular elements form a broad carapace with some detached scutes on the flanks. Some *P. trigonatus* lose the median pair of scutes in PC 2 to PC 5 in various combinations. This character is unique among the living Crocodilia. Our interpretation of *P. trigonatus* is based on the fact that it is less ossified than *P. palpebrosus*. In *P. palpebrosus* PC 18 usually has four elements, while in *P. trigonatus* there are usually two. PC 19 is reduced and has two elements in *P. palpebrosus*. In *P. trigonatus* a single transverse row of the cervical shield is lacking; and, on the

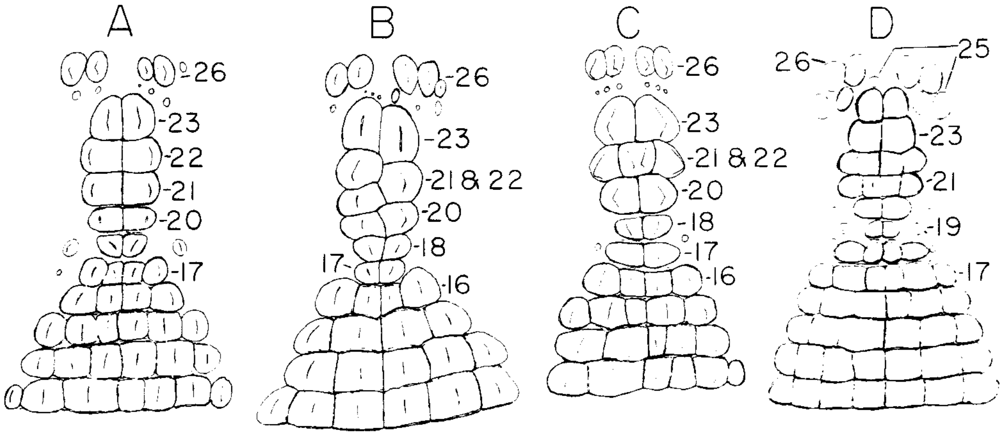

Figure 10. Anterior end of the dorsal armor, PC 13 forward, with selected precaudal scale rows numbered on: A. *Paleosuchus trigonatus*, FMNH 69878. B. *P. trigonatus*, FMNH 69882. C. *P. trigonatus*, FMNH 69877. D. *P. palpebrosus*, FMNH 134989.

basis of its small size in *P. palpebrosus*, we believe the missing row to be PC 19. PC 20 to PC 23 normally have two elements. In some individuals PC 21 and PC 22 appear to be compound. The nape has one well-developed row, PC 26, and small scales lie between PC 26 and PC 23, arranged in one or more additional rows. The larger of these latter small rows is probably PC 24, because this row is better developed in *P. palpebrosus*. Some *P. trigonatus* and *P. palpebrosus* combine median scute pairs in the neck to form median unpaired single or double keeled elements. This again is unique among the living Crocodilia.

DISCUSSION

The Fossil Record

The presence of middorsal armor is widespread in the early archosaurs and their descendants, although it is lacking or poorly developed in the most primitive thecodonts, the proterosuchians (Reig, 1970; Romer 1972). It is most highly developed in parasuchians (phytosaurs), aetosaurs, certain ornithischians, and, of course, crocodilians. In some of these, such as parasuchians (Chatterjee, 1978) and *Stagonolepis* (Walker, 1961) there is also a one-to-one correspondence between vertebrae and transverse scute rows. The wide occurrence of dorsal armor suggests that it is primitive for archosaurs; its general absence in proterosuchians, however, urges caution in accepting this hypothesis.

Fossil crocodilians with dorsal armor in place are rare, but several good examples exist. The earliest known true crocodiles, *Protosuchus* (Colbert and Mook, 1951), from the Upper Triassic or earliest Jurassic, and *Orthosuchus* (Nash, 1975), from the Upper Triassic, have essentially identical dorsal armor. In the neck and trunk region paired rectangular scutes occur in one-to-one correspondence with the vertebrae. At their lateral edges the scutes are sharply downturned to form a lateral face. Behind the occiput an extra small scute or scute pair (corresponding to the proatlas?) occurs. In the more completely known *Protosuchus* this armor extends onto the tail to its tip. The armor forms a long, essentially parallel sided, rigid bony adjunct to the vertebral column (Fig. 3A). The armor of another early crocodilian, *Stegomosuchus*, seems to be much the same (Walker, 1968). Protosuchian dorsal armor did not form a carapace, though the scutes did enclose the epaxial musculature, and as such were protective.

Romer (1974) derived crocodilians from creatures of amphibious habits because strong hind limbs and tails function well in aquatic environments. Nash (1975) followed Romer, supposing that *Orthosuchus* spent much of its time in the water. However, the completeness of the dorsal armor of protosuchian crocodiles would have prohibited tossing the head upwards and backwards for swallowing prey while keeping the gullet above water in modern crocodilian fashion. Protosuchians could not feed in deep water, and also lacked a compressed tail with a median keel (see Manter, 1940, on the importance of the tail in swimming). We suggest that the group was terrestrial.

The transition from protosuchian to mesosuchian crocodiles involved reduction or loss of the anteriormost transverse scute rows and lateral compression of the posterior half of the tail to a vertical keel. The development of a caudal keel and loss of the anteriormost transverse rows (thus gaining the ability to toss the head backwards to swallow) indicate aquatic habits.

Some mesosuchians retained a parallel sided armor much like that of protosuchians (atoposaurs, Wellnhoffer, 1971), while others broadened the scutes in the trunk region (e.g., *Teleosaurus*, Kälin, 1955). Many mesosuchians had peg and socket articulations on the lateral edges of their scutes. This is an elaboration of peglike processes seen in *Protosuchus* and *Orthosuchus*. Most mesosuchians still had only a single pair of scutes per transverse row (Romer, 1956). The pelagic marine thalattosuchians lacked armor altogether (Troxell, 1925). (It is interesting that the most reduced dorsal armor in modern crocodilians occurs in the two most marine species, *Crocodylus porosus* and *C. acutus*.)

The transition from mesosuchian to eusuchian crocodiles involved further caudal compression, and, in some cases, further loss of anterior transverse scute rows. Eusuchians broadened and fractured the ancestral scute pairs into paired sets of two to six elements each (Fig. 3B, C), lost the lateral peg and socket articulations and consequent rigidity, and covered the trunk and base of the tail with a pavement of bony plates forming a defensive carapace. Interruption or narrowing of the armor in the shoulder region is also typical of eusuchians (Fig. 3C, 4). In general, eusuchian armor is broader and more flexible than that of their mesosuchian predecessors, with a tendency towards interruption of the dorsal armor in the shoulder region. *Procaimanoidea (Hassiacosuchus)* (Mook, 1941), *Leidyosuchus* (Erickson, 1976), and *Bernissartia* (Kälin, 1955)[1] are fossil eusuchians whose armor is known, and all are of essentially modern form. Among the living Eusuchia, the dorsal armor of *Gavialis* is most reminiscent of mesosuchian armor.

VARIATION AND EVOLUTION

Primitively, crocodilian dorsal armor consists of 27 transverse precaudal rows of two scutes each, as is found in protosuchians. The preceding review of historical changes in the primitive armor, through mesosuchian and eusuchian stages, allows us to make some general statements on the direction of evolution of some characters. Advanced characteristics include loss of rows, a greater number of scutes per row, broadening of the trunk armor, and narrowing of the armor

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[1] Buffetaut (1975) has questioned whether *Bernissartia* is a eusuchian on the basis of palatal and vertebral structure; its armor, however, is unquestionably advanced in character.

at the cervico-thoracic juncture. With this in mind, we can look at evolutionary steps and directions in the living taxa. The possibility of reversal cannot be ignored; for example, the low number of scutes per row in *Crocodylus acutus* is probably a secondary loss.

The variation in dorsal armor among the living crocodilians shows that a variety of evolutionary changes have occurred within the group. The two kinds of changes which account for most of this variation are deletion of rows, and the compounding of rows in the cervical region.

Deletion of at least the anteriormost precaudal row (PC 27) occurs in all modern taxa. In most taxa more are missing. In the genus *Crocodylus* a series of stages (not necessarily a phyletic series) in the reduction of armor at the cervico-thoracic juncture can be seen. *C. cataphractus* has continuous precaudal armor through PC 22+23 (Fig. 5D). In *C. johnstoni*, PC 18 and PC 19 may be reduced to a single scute (Fig. 6A). In *C. niloticus* reduction continues, with one or both of PC 18 and PC 19 entirely absent, leaving the precaudal armor continuous to PC 17 and the cervical and thoracic armor discontinuous (Fig. 6B-D). Further rows may be deleted, so that in *C. acutus*, for example, some individuals have continuous armor only to PC 14. Deletion may also occur in the cervical shield, and the presence of rows usually absent also occasionally occurs as an individual variation.

The compounding of rows, which entails a loss of one-to-one correspondence of vertebrae and transverse rows, is clearly derived with respect to separate rows being present. Compounding is indicated by the occurrence of individuals showing asymmetrical fusion. This is clearly seen in the series of *Tomistoma* in Fig. 5: 5A has the enlarged compound, 5B is compound only on the left, and 5C has both PC 22 and PC 23 entirely separate. Though greatly enlarged scutes, and scutes which overlie two vertebrae suggest compounding, the recognition of compounding depends on individual variation. Some species may be phenotypically fixed for compounds, which would make the compound row difficult to detect.

Overall development of the dorsal armor is reflected in the number of rows present and the number of scutes per row. There is considerable variation among species in the extent to which the armor is developed. In the genus *Paleosuchus*, for example, *palpebrosus*, with more well-developed armor, has 24 continuous precaudal rows and a mode of eight scutes per row at midbody, while the less armored *trigonatus* lacks PC 19, and has modally six scutes per row. Similarly, *Crocodylus rhombifer* has at least 17 continuous precaudal rows and six scutes per row, while *C. acutus* usually has 16 or fewer continuous precaudal rows, and four scutes per row. Overall reduction of armor is sometimes accompanied by marked left/right asymmetries, as in *C. acutus* and *C. moreletii*.

The variation within species is of the same sort as that which distinguishes species. Thus, species differ in number of transverse rows, number of scutes per transverse row, and the presence of compounds, and all of these characters vary within species. Many individual variations are reversions to a more primitive condition, such as the breakup of compounds in *Crocodylus niloticus*, or the presence of PC 17 in some *C. acutus*. Other variations are derived and characteristic of more advanced species, such as the occasional reduction of PC 18 and PC 19 in the relatively primitive *C. johnstoni*. Some individuals show phenotypes more derived than those characteristic of even the most advanced species, such as a *C. niloticus* with a very reduced cervical shield, or a *C. acutus* with only 14 continuous precaudal rows.

ACKNOWLEDGMENTS

About fifteen years ago, one of us (FDR) brought a young crocodilian to the Museum of Comparative Zoology for

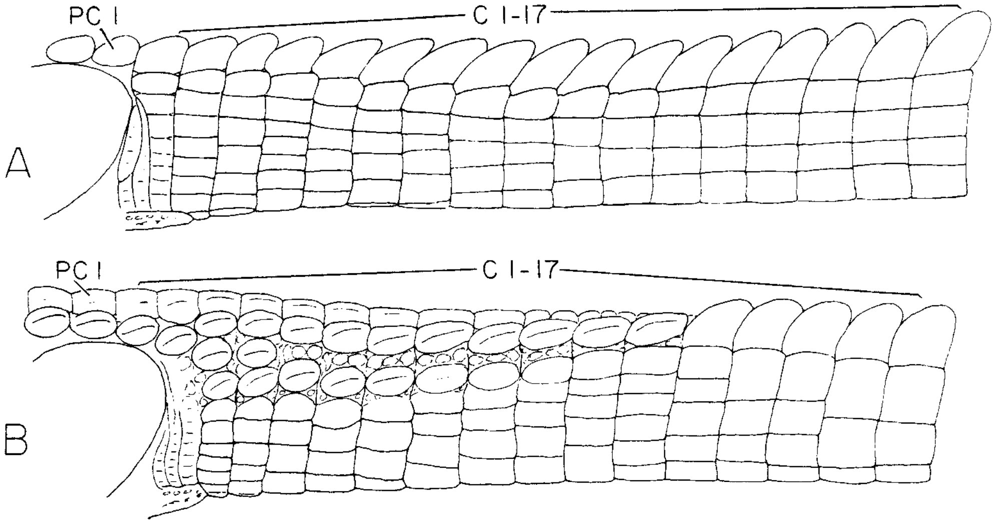


Figure 11. Lateral views of the anterior ends of the tails of: A. *Tomistoma schlegelii*, MCZ 9327, showing absence of basicaudal irregularity. B. *Osteolaemus tetraspis*, MCZ 2107, showing two thick granular strips separating the dorsal from the ventrolateral scalation.

identification. The beast had been sold as *Crocodylus acutus*, but appeared to differ from that taxon by the number of osseous scutes on the neck. Ernest E. Williams ducked the question, suggesting that crocodiles were not yet understood, and that work should be done on the problem. We thank him for inspiring and facilitating the bulk of this work.

We report primarily on specimens in the American Museum of Natural History (AMNH), the Field Museum of Natural History (FMNH), the Museum of Comparative Zoology (MCZ), and the National Museum of Natural History (USNM). We have also examined specimens in the Boston Museum of Science (BMS), the California Academy of Sciences (CAS), the Museo Nacional de Historia Natural Santo Domingo, (MNHNSD), the Instituto de Historia Natural (Tuxtla Gutierrez, Chiapas), the National Museum of Canada, and the Yale Peabody Museum. We are indebted to the curators and staffs of these institutions, especially Ernest E. Williams, Hymen Marx, Miguel Alvarez del Toro, George Zug, Charles A. Ross, and the late James A. Peters. We are also indebted to Aleta Karstad for Figure 4, Jim Lovesek for photographs of *Crocodylus intermedius*, and E. E. Williams and Don McAllister for radiographs. In addition, we thank A. S. and S. B. Avery, J. M. Clark, F. R. Cook, P. Elias, K. Miyata, A. Rhodin, J. P. Rosado, J. P. Ross, F. W. and A. K. Schueler, and R., R., and F. Whiston. F.D.R. was supported in part by a grant from the Ella Lyman Cabot Trust, and G.C.M. was supported by an NSF graduate fellowship and NRM.

APPENDIX: SPECIMENS EXAMINED

Museum abbreviations are in the Acknowledgments. Numbers in parentheses are the number of individuals in lots designated by a single museum number.

TABLE 1. NUMBER OF CONTIGUOUS SCUTES PER TRANSVERSE ROW IN PC 1-PC 18.
Number given is mode (or modes) with range underneath in parentheses. Species are identified by the first four letters of their generic and specific names. N = sample size.

Species	N	PC 1	PC 2	PC 3	PC 4	PC 5	PC 6	PC 7	PC 8	PC 9
Gavi gang	8	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)
Tomi schl	12	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4–6)	6 (6)	6 (5–6)	6 (6–7)
Croc cata	11	4 (4)	4 (4)	4 (4)	4 (4–5)	6 (4–6)	6 (4–6)	6 (4–6)	6 (4–8)	6 (4–7)
Croc john	11	4 (4)	4 (4)	4 (4)	4 (3–5)	4,6 (4–6)	6 (6)	6 (6)	6 (6)	6 (6)
Croc nilo	19	4 (4)	4 (4)	4 (4–6)	6 (4–6)	6 (4–6)	6 (4–6)	6 (4–8)	6 (6–8)	6 (6–8)
Croc palu	12	4 (4)	4 (4)	4 (4–5)	4 (4–6)	6 (4–6)	6 (5–6)	6 (6–7)	6 (4–7)	4,5 (4–8)
Croc siam	6	4 (4)	4 (4)	4 (4)	4 (4–6)	6 (4–7)	6 (6–7)	6 (5–8)	5 (4–8)	6 (5–6)
Croc poro	12	4 (4)	4 (4)	4 (4–6)	6 (4–6)	6 (4–6)	6 (6–8)	8 (6–8)	6 (6–8)	6 (6–8)
Croc nova	14	4 (4)	4[l] (4)	4[k] (4–5)	6 (4–6)	6 (6)	6 (6–8)	8[l] (6–8)	8 (8)	8[i] (6–11)
Croc rhom	6	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	6 (5–6)	6 (6)	6 (6)	6 (6–7)
Croc more	8	4 (3–5)	4 (4)	4 (3–4)	4 (3–5)	4 (3–5)	4 (2–6)	3 (3–6)	6 (2–6)	6 (4–6)
Croc acut	37	4 (3–5)	4 (2–4)	4 (2–4)	4 (2–4)	4 (2–5)	3,4 (2–6)	4 (2–6)	3 (2–6)	4 (2–6)
Croc inte[a]	2	4,5	4	4	4	5,6	5	5,6	6	5
Oste tetr	18	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4–6)	4 (4–6)	6 (4–6)	6 (4–7)
Alli sine	14	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4)	4 (4–6)	6 (4–6)	6 (6–8)
Alli miss	17	4 (4)	4 (4)	4 (4)	4 (4–6)	4 (4–6)	6 (4–6)	6 (5–7)	6[j] (6–8)	6 (6–8)
Caim lati	12	4 (4–6)	4[i] (4)	4[i] (4)	4 (4)	6 (5–6)	6 (6)	6[i] (6–8)	8 (4–9)	8 (5–9)
Caim croc	24	4[o] (4–6)	4[o] (4–6)	4[o] (4–6)	6[o] (4–8)	6[o] (6–10)	8[o] (6–11)	8 (7–12)	8 (8–12)	8 (8–12)
Mela nige	15	6 (6)	6 (5–6)	6 (6)	6 (6)	8 (6–8)	8 (8–10)	8 (8–10)	10 (8–12)	10 (9–11)
Pale palp	5	4 (4)	4[c] (4)	4 (4)	4 (4)	4 (4)	4,5 (4–6)	6[c] (6–8)	7 (6–7)	8[b] (6–9)
Pale trig	25	4 (4)	4[o] (2–4)	2 (2–4)	2 (2–4)	4 (4–5)	4 (4–5)	4[o] (3–6)	5 (4–6)	6 (4–7)

TABLE 1. CONTINUED.

Species	N	PC 10	PC 11	PC 12	PC 13	PC 14	PC 15	PC 16	PC 17	PC 18
Gavi gang	8	4	4	4	4[d]	4[d]	4[d]	4[d]	4[d]	4[c]
		(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)	(4)
Tomi schl	12	6	6	6	6[g]	4[g]	4[g]	4[g]	4[g]	2[g]
		(6–8)	(6–8)	(5–7)	(5–6)	(4–6)	(4–6)	(4)	(4)	(2–4)
Croc cata	11	6	6	6	6[f]	6[f]	6[f]	6[f]	4	2[f]
		(4–6)	(5–8)	(4–7)	(5–7)	(6)	(6)	(2–6)	(2–4)	(1–4)
Croc john	11	6	6	6	6	6	6	6	4	2
		(6)	(6–7)	(6–7)	(6–7)	(6)	(6)	(4–6)	(2–4)	(1–2)
Croc nilo	19	6	6	6	6	6	6	6	2	0
		(4–8)	(5–8)	(6–9)	(6–8)	(4–8)	(3–7)	(0–6)	(0–4)	(0)
Croc palu	12	4,5,6	5	6	6	6	6	4	2	0
		(4–6)	(4–6)	(4–6)	(4–7)	(6–7)	(2–6)	(3–5)	(0–4)	(0)
Croc siam	6	6	6	6	6	6	6	4	2	0
		(4–6)	(5–7)	(6–7)	(5–7)	(6)	(6)	(4–6)	(0–4)	(0–2)
Croc poro	12	6	6	6	6[j]	6[j]	6[j]	2[j]	0[j]	0[j]
		(6–8)	(6–8)	(6–7)	(6–8)	(4–6)	(0–6)	(0–4)	(0–4)	(0)
Croc nova	14	8[i]	8[i]	8	8[m]	8[k]	6[k]	6[k]	4[k]	0[k]
		(8–12)	(7–11)	(8–9)	(6–8)	(6–8)	(6)	(4–6)	(0–5)	(0)
Croc rhom	6	6	6	6	6	6	6	6	4	0,1,2
		(6)	(6)	(6)	(6)	(6)	(6)	(6)	(2–6)	(0–2)
Croc more	8	4	4	4	2	6	4	2	0	0
		(2–6)	(4–6)	(3–6)	(2–6)	(2–6)	(2–6)	(2–4)	(0)	(0)
Croc acut	37	3	4	4	3	2	2	2	0	0
		(2–5)	(2–4)	(2–5)	(0–4)	(2–5)	(0–6)	(0–4)	(0–2)	(0)
Croc inte[a]	2	5,6	5,6	6	6	6	6	4	0	0
Oste tetr	18	6	6	6	6	6	6	6	4	2
		(4–8)	(4–7)	(4–8)	(6)	(5–7)	(6)	(4–6)	(2–6)	(0–4)
Alli sine	14	6	6	6,7	6	6	6	6	4	0
		(6–8)	(6–8)	(6–8)	(6–8)	(4–6)	(4–6)	(4–6)	(0–5)	(0–2)
Alli miss	17	6	8	8	8	6	6	6	6	2
		(6–8)	(5–8)	(6–8)	(6–8)	(6–8)	(4–6)	(4–6)	(4–6)	(2–6)
Caim lati	12	6	6	6	6[i]	6	6	6	4	2[e]
		(6–9)	(5–8)	(6–8)	(6–7)	(5–8)	(4–6)	(4–6)	(2–6)	(2–4)
Caim croc	24	8	8	8,9	8	8	6	6	4	2[n]
		(8–12)	(6–12)	(6–11)	(6–11)	(6–10)	(5–8)	(6–8)	(2–6)	(0–6)
Mela nige	15	10	10[h]	10[h]	10[h]	10	10	8	6	6
		(10–11)	(9–12)	(9–11)	(9–11)	(9–11)	(8–10)	(7–10)	(6–8)	(4–6)
Pale palp	5	8	7,8	8[c]	6	6	6	6	6	4
		(6–8)	(6–8)	(6–8)	(6–8)	(6–7)	(6)	(5–7)	(4–6)	(3–6)
Pale trig	21	6	6	5,6[o]	6[o]	5[o]	4[o]	4[o]	4[o]	2[o]
		(4–6)	(4–7)	(4–8)	(4–7)	(4–6)	(4–6)	(2–6)	(0–4)	(2–4)

[a] Range not given since N=2. [b] N=6 [c] N=9 [d] N=10 [e] N=11 [f] N=12 [g] N=13 [h] N=14 [i] N=15 [j] N=16 [k] N=18 [l] N=19 [m] N=21 [n] N=23 [o] N=25

TABLE 2. NUMBER OF DOUBLE AND SINGLE CREST CAUDALS IN UNDAMAGED SPECIMENS OF LIVING CROCODILIANS. Species are identified by the first four letters of their generic and specific names.

	Number of double crest caudals													Number of single crest caudals									
Species	9	10	11	12	13	14	15	16	17	18	19	20	21	16	17	18	19	20	21	22	23	24	25
Gavi gang										3	2								1	1			
Tomi schl									1	7	3						2	6	2				
Croc cata								5	7					2	1	2	1	1	3	1			
Croc john									10	2						2	1	3					
Croc nilo								1	6	9	8		1		1				6	6			
Croc palu									2	8	2	1		1	5	2	1						
Croc siam										1	3	2				1		1	2				
Croc poro											3	7	9				2	1	3	3			
Croc nova										7	11	2				6	6	3					
Croc rhom										3	4			1	1	1							
Croc more									3	4	1					1	2	1	1				
Croc acut								1	7	8	15	5		1	20	17	2						
Croc inte[a]									1	9	1				3	4	2						
Oste tetr		1	4	9	3	1									2	4	5	2					
Alli sine							2	8	3											4	3	4	
Alli miss										6	11					1			6	2	3		
Caim lati					3	9	2		1											1	1	4	3
Caim croc			1	3	2	13	4	1											3	7	5	3	
Mela nige								1	8	6										1	3	3	2
Pale palp	1	5	3																1				
Pale trig	2	21	2											2	4	2	1						

[a] Data from Medem, 1958a, Table 1. The single specimen of this species available to us was also examined by Medem. Medem's last dorsal corresponds to PC 1 in this specimen; thus, his counts correspond to the method used in this paper.

TABLE 3. FORMATION OF Y-SHAPED CAUDAL KEEL FROM PELVIC KEEL ROWS.

Median pelvic keel rows merge with lateral pelvic keel row to become Y-shaped caudal keel	Median pelvic keel rows do not contribute to the Y-shaped caudal keel	
	Median pelvic keel rows become an unpaired median keel row diminishing posteriorly	Median pelvic keel rows maintain their paired nature until diminishing posteriorly
Paleosuchus, Alligator sinensis	*Caiman, Melanosuchus*	*Gavialis, Tomistoma, Crocodylus, Osteolaemus, Alligator mississippiensis*

TABLE 4. OCURRENCE OF FOUR KINDS OF BASICAUDAL IRREGULARITIES IN EXAMINED SPECIMENS OF LIVING CROCODILIANS.

The irregularities are further described in the Methods. + = present; − = absent; * = thinner than in other species. Species are identified by the first four letters of their generic and specific names.

Species	One thin granular strip	One or more thick strips	Lateral intrusions	Ventrolateral intrusions
Gavi gang	−	−	−	−
Tomi schl	−	−	−	−
Croc cata	+/−	−	−	−
Croc john	+/−	−	−	−
Croc nilo	*/−	−	−	−
Croc palu	+/−	+/−	−	−
Croc siam	+/−	+/−	−	−
Croc poro	+/−	+/−	+/−	−
Croc nova	+/−	−	+/−	−
Croc rhom	−	−	−	−
Croc more	*/−	−	+/−	+
Croc acut	+/−	*/−	−	−
Croc inte	−	−	+/−[a]	−
Oste tetr	−	+/−	+/−	−
Alli sine	−	−	+/−	−
Alli miss	−	−	+/−	+/−
Caim lati	−	+/−	+/−	−
Mela nige	*/−	−	+	−
Pale palp	−	−	+/−	−
Pale trig	−	+/−	−	−

[a] C. A. Ross, personal comminication.

Gavialis gangeticus. INDIA: AMNH 81802, MCZ 5263, 161013, USNM 136615; NO LOCALITY: AMNH 48500, BMS no #, FMNH 82681, no #(2), USNM 211524.

Tomistoma schlegelii. MALAYSIA: USNM 84247, 85106; SUMATRA: FMNH 11084–5, MCZ 9327, USNM 58136, 65509–10, 145586–8; NO LOCALITY: AMNH 66380, 101422, FMNH 134997, 206755, USNM no #.

Crocodylus cataphractus. ANGOLA: MCZ 29360; TANZANIA: MCZ 54650, 54751; ZAIRE: AMNH 10076, 45863, MCZ 16732; NO LOCALITY: AMNH 2206, 6584, 7293, 8877, FMNH 37213, MCZ 5456, USNM 60578.

Crocodylus johnstoni. AUSTRALIA: AMNH 82535, 86536–7, 86539, MCZ 35001–4, 35006, 111978, USNM 64090–1; NO LOCALITY: AMNH 93743.

Crocodylus niloticus. BOTSWANA: USNM 195448, 195782–3; CAMEROON: FMNH 190827–9; CHAD: MCZ 27070–1; ETHIOPIA: USNM 42860, 136621; GHANA: MCZ 55153; KENYA: MCZ 40001, USNM 63592; MADAGASCAR: MCZ 2114, 5461, 12552, 16729–31, 16868; MALAWI: MCZ 30000; MALI: FMNH 20799; SIERRA LEONE: MCZ 54120; SOUTH AFRICA: FMNH 17155; TANZANIA: MCZ 48000.

Crocodylus palustris. INDIA: AMNH 2413–8, FMNH 31538, 63739; SRI LANKA: MCZ 42176, 42180; NO LOCALITY: AMNH 45099, FMNH 95995, MCZ 6753, 17595–7.

Crocodylus siamensis. THAILAND: MCZ 3716, 20301, USNM 79476; NO LOCALITY: AMNH 75035, USNM 3906, 8893.

Crocodylus porosus. AUSTRALIA: AMNH 86541; INDONESIA (IRIAN JAYA): AMNH 62041–2; INDONESIA (SUMATRA): MCZ 43742; PAPUA NEW GUINEA: MCZ 110450–1, 142950, USNM 211310; PHILIPPINES: FMNH 14346, 52363–4, USNM 38081; SANTA CRUZ IDS.: AMNH 42162; SOLOMON IDS.: MCZ 72936; THAILAND: USNM 72730–6; NO LOCALITY: AMNH 66388.

Crocodylus novaeguineae. PAPUA NEW GUINEA: CAS 119186–7, 121997–8; MCZ 65284–5, 101338, 120335, 140805–7, USNM 211297, 211305–6, 082826–7 (field numbers); PHILIPPINES: FMNH 52357–60, 52362; NO LOCALITY: USNM 083141(field number).

Crocodylus rhombifer. CUBA: FMNH 34677, MCZ 1249, 1397, 12081, 33394, USNM 13576; NO LOCALITY: AMNH 77595.

Crocodylus moreletii. BELIZE: FMNH 4430,

49369, MCZ 18856; GUATEMALA: USNM 71954, 71957–8; MEXICO: MCZ 8047, 53860, USNM 115357; NO LOCALITY: MCZ 17583.

Crocodylus acutus. COLOMBIA: MCZ 17610; CUBA: MCZ 1250, 12278, 17718; DOMINICAN REPUBLIC: MNHNSD no #(8); HAITI: MCZ 1339, 3596(3), USNM 80892; JAMAICA: MCZ 6093(7), 42981, 44853; MEXICO: FMNH 23147; NICARAGUA: MCZ 5454, USNM 15230; PANAMA: MCZ 1010, 1265, 2003, 2720, 7318, 18927–9, 28051; UNITED STATES: MCZ 13428–30, 13432.

Crocodylus intermedius. COLOMBIA: FMNH 75658.

Osteolaemus tetraspis. CAMEROON: MCZ 29348–9, 33594; CONGO: USNM 62226; GHANA: USNM 207060; LIBERIA: AMNH 82166–7, 116354, MCZ 22913, USNM 58273, 193289; NIGERIA: MCZ 2017; ZAIRE: AMNH 29889, MCZ 12458, 42855–6; NO LOCALITY: AMNH 7766, 24740, MCZ no #.

Alligator sinensis. CHINA: AMNH 28689, 28691–3, FMNH 38234, 38236, MCZ 16706–8, 17545–6, 17548–50, 42982, 161014, USNM 72846.

Alligator mississippiensis. UNITED STATES: MCZ 969, 3767, 13433–4, 16715, 17723, 26949, 159136, 159146–7; NO LOCALITY: MCZ 5458, 17592–3, 159149–52.

Caiman latirostris. ARGENTINA: FMNH 9707–8; BRAZIL: FMNH 5777, MCZ 1151, 1455, 2854, 3588–9, 3769, 17600, 17716, 29099, 159154, USNM 98780; PARAGUAY: MCZ 34226.

Caiman crocodilus. BOLIVIA: AMNH 97310, 97315–23, FMNH 81564–5; BRAZIL: AMNH 87939, MCZ 1241, 2606, 3394, 3972, 3975; COSTA RICA: MCZ 15333–4, 54997; GUYANA: FMNH 26682; MEXICO: MCZ 5040, 17581; PANAMA: FMNH 13402, MCZ 2035 2721, 20566, 22332–3, 29760; SURINAM: MCZ 154922; NO LOCALITY: AMNH 66393.

Melanosuchus niger BOLIVIA: AMNH 97324; BRAZIL: MCZ 1011, 2547–9, 3590, 3592, 15134, 17598, 17726, 51851, 160240, no #; NO LOCALITY: AMNH no #(2).

Paleosuchus palpebrosus. BOLIVIA: AMNH 97328; BRAZIL: AMNH 16574, 97326–7, MCZ 2928, USNM 149134; COLOMBIA: FMNH 69867, 69869, 69875, 134989; NO LOCALITY: MCZ 160000.

Paleosuchus trigonatus. BRAZIL: AMNH 101056, MCZ 2957, 3785; COLOMBIA: FMNH 69877–8, 69881–2; ECUADOR: AMNH 61548–51, 72470, 113635, MCZ 84029; GUYANA: AMNH 16048, 61513, 61516–8, 64823–5; NO LOCALITY: AMNH 46281–2, 159384.

HYBRID: presumed *Crocodylus acutus* × *C. rhombifer* CUBA: AMNH 82943. Counts from this animal or any other presumed hybrids mentioned in the text are not included in Tables 1–4.

LITERATURE CITED

ANONYMOUS. 1969. Cuban crocodile. Animal Kingdom, **72**(5): 29.

BOULENGER, G. A. 1889. Catalogue of the chelonians, rhynchocephalians, and crocodiles in the British Museum (Natural History). London, Taylor and Francis.

BRAZAITIS, P. 1973 (1974). The identification of living crocodilians. Zoologica, **58**: 59–101.

BREDER, C. M., JR. 1947. An analysis of the geometry of symmetry with especial reference to the squamation of fishes. Bull. Amer. Mus. Nat. Hist., **88**: 321–412.

BUFFETAUT, E. 1975. Sur l'anatomie et la position systématique de *Bernissartia fagesii* Dollo, L., 1883, crocodilien du Wealdien de Bernissart, Belgique. Bull. Inst. r. Sci. Nat. Belg., **51**: 1–20.

CHATTERJEE, S. 1978. A primitive parasuchid (phytosaur) from the Upper Triassic Maleri Formation of India. Palaeontology, **21**: 83–127.

COLBERT, E. H., AND C. C. MOOK. 1951. The ancestral crocodilian *Protosuchus*. Bull. Amer. Mus. Nat. Hist., **97**: 143–182.

CUVIER, G. 1807. Sur les différentes espèces de crocodiles vivans et sur leurs caractères distinctifs. Ann. Mus. Hist. Nat. Paris, **10**: 8–66.

———. 1831. The animal kingdom arranged in conformity with its organization. Vol. 9. The class Reptilia. London, Whittaker, Treacher.

DERANIYAGALA, P. E. P. 1939. The tetrapod reptiles of Ceylon. Vol. 1. Testudinates and crocodilians. Ceylon J. Sci. Colombo Mus. Nat. Hist. Ser.

DUMÉRIL, A. M. C., AND G. BIBRON. 1836. Erpétologie génerále ou histoire naturelle complète des reptiles. Vol. 3. Paris.

ERICKSON, B. R. 1976. Osteology of the early eusuchian crocodile *Leidyosuchus formidabilis*, sp. nov. Monogr. Sci. Mus. Minnesota, Paleontology, **2**: 1–61.

FOX, S. F. 1975. Natural selection on morphological phenotypes of the lizard *Uta stansburiana*. Evolution, **29**: 95–107.

GADOW, H. F. 1901. Amphibia and reptiles. The Cambridge Natural History Vol. 8. London, Macmillan.

HECHT, M. K. 1952. Natural selection in the lizard genus *Aristelliger*. Evolution, **6**: 112–124.

HIGGINS, G. M. 1923. Development of the primitive reptilian vertebral column, as shown by a study of *Alligator mississippiensis*. Amer. J. Anat., **31**: 373–407.

HOFFSTETTER, R., AND J.-P. GASC. 1969. Vertebrae and ribs of modern reptiles, pp. 201–310. *In* C. Gans, A. d'A. Bellairs and T. S. Parsons (eds.), Biology of the Reptilia, Vol. 1. London, Academic Press.

HUXLEY, T. H. 1859. On the dermal armour of *Jacare* and *Caiman*, with notes on the specific and generic characters of recent Crocodilia. J. Proc. Linn. Soc. Zool. Lond., **4**: 1–28.

Kälin, J. 1955. Crocodilia, pp. 695–784, *In* J. Piveteau (ed.), Traité de Paléontologie, Vol. 5. Paris, Masson.

Kerfoot, W. C. 1970. The effect of functional changes upon the variability of lizard and snake body scale numbers. Copeia, **1970:** 252–260.

Manter, J. T. 1940. The mechanics of swimming in the alligator. J. Exp. Zool., **83:** 345–358.

Medem, F. J. 1958a. Informe sobre reptiles Colombianos, III. Investigaciones sobre la anatomia craneal, distribucion geograficá y ecología de *Crocodylus intermedius* (Graves) en Colombia. Caldasia, **8:** 175–215.

———. 1958b. The crocodilian genus Paleosuchus. Fieldiana, Zoology, **39:** 227–247.

———. 1970. Sobre un hibrido inter-especifico del genero *Paloosuchus* (Crocodylia. Alligatoridae). Rev. Acad. Colombiana de Cien, Exactas Fis. y Nat., **13:** 467–479.

Miller, W. E. 1980. The late Pliocene Las Tunas local fauna from southernmost Baja California, Mexico. J. Paleontology, **54:** 762–805.

Mook, C. C. 1941. A new crocodilian, *Hassiacosuchus kayi*, from the Bridger Eocene Beds of Wyoming. Ann. Carnegie Mus., **28:** 207–221.

Nash, D. S. 1975. The morphology and relationships of a crocodilian, *Orthosuchus stormbergi*, from the Upper Triassic of Lesotho. Ann. S. Afr. Mus., **67:** 227–329.

Reig, O. A. 1970. The Proterosuchia and the early evolution of the archosaurs; an essay about the origin of a major taxon. Bull. Mus. Comp. Zool., **139:** 229–292.

Romer, A. S. 1956. Osteology of the reptiles. Chicago, Univ. Chicago Press.

———. 1972. The Chañares (Argentina) Triassic reptile fauna. XII. The postcranial skeleton of the thecodont *Chanaresuchus*. Breviora Mus. Comp. Zool. No. 385, pp. 1–21.

———. 1974. Aquatic adaptation in reptiles—primary or secondary? Ann. S. Afr. Mus., **64:** 221–230.

Ross, C. A., and C. D. Roberts. 1979. Scalation of the American alligator. U.S. Dept. Int. Fish and Wildl. Serv. Spec. Sci. Rep.—Wildl. No. 225.

Ross, C. A., and F. D. Ross. 1974. Caudal scalation of Central American *Crocodylus*. Proc. Bio. Soc. Wash., **87:** 231–233.

Schmidt, K. P. 1956. On the status and relations of *Crocodylus mindorensis*. Fieldiana, Zoology, **33:** 535–539.

Seidel, M. R. 1979. The osteoderms of the American alligator and their functional significance. Herpetologica, **35:** 375–380.

Troxell, E. L. 1925. *Hyposaurus*, a marine crocodilian. Amer. J. Sci., **9:** 489–514.

Varona, L. S. 1966. Notas sobre los crocodílidos de Cuba y descripción de una nueva especie del Pleistoceno. Poeyana Ser. A, **16:** 1–34.

Walker, A. D. 1961. Triassic reptiles from the Elgin area: *Stagonolepis*, *Dasygnathus* and their allies. Phil. Trans. Roy. Soc. Lond. Ser. B, **244:** 103–204.

———. 1968. *Protosuchus*, *Proterochampsa*, and the origin of phytosaurs and crocodiles. Geol. Mag., **105:** 1–14.

Wellnhoffer, P. 1971. Die Atoposauridae (Crocodylia, Mesosuchia) der Oberjura—plattenkalke Bayerns. Palaeontographica Abt. A, **138:** 133–165.

Wermuth, H. 1953. Systematik der rezenten krokodile. Mitteil. Zool. Mus. Berlin, **29:** 375–514.

Wermuth, H., and R. Mertens. 1961. Schildkroten, krokodile, bruckenechsen. Gustav Fischer Verlag, Jena.

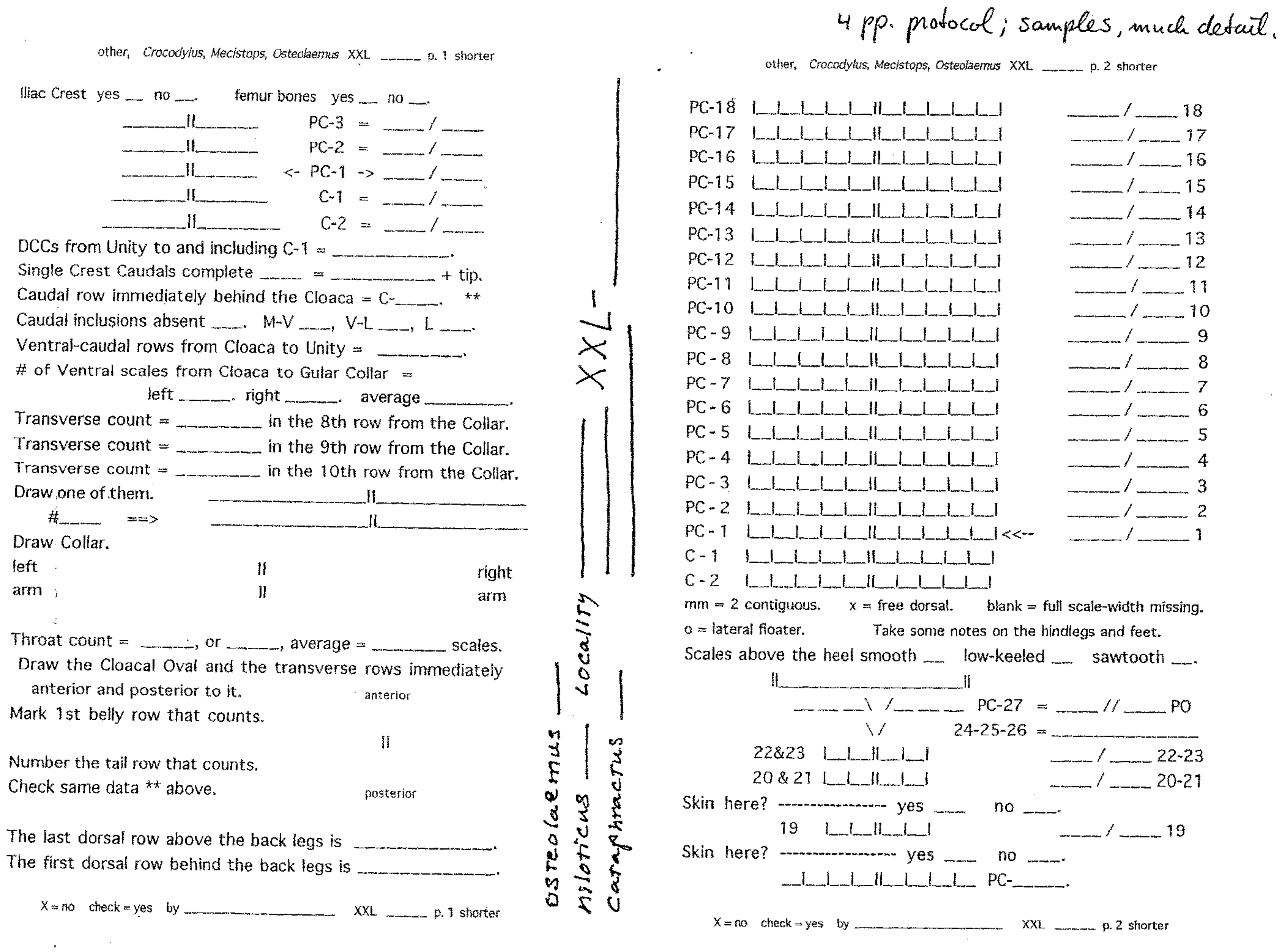
——— and ———. 1977. Liste der rezenten amphibien und reptilien. Testudines, Crocodylia, Rhynchocephalia. Das Tierreich 100.

Williams, E. E. 1959. Gadow's arcualia and the development of tetrapod vertebrae. Quart. Rev. Bio., **34:** 1–32.

Youngprapakorn, U. 1976. Samutprakan, Thailand. Borpit, Thailand.

Erratum: Figure 1B (MCZ 3589) is *Caiman latirostris*.

ANNEXURE B – FIELD-PROTOCOLS USED FOR THE 2006-2007 FIELD-SAMPLE



other, *Crocodylus, Mecistops, Osteolaemus* XXL _____ p. 1 shorter

Iliac Crest yes __ no __. femur bones yes __ no __.

_______||_______ PC-3 = _____ / _____

_______||_______ PC-2 = _____ / _____

_______||_______ <- PC-1 -> _____ / _____

________||________ C-1 = _____ / _____

_________||_________ C-2 = _____ / _____

DCCs from Unity to and including C-1 = ____________.

Single Crest Caudals complete _____ = ____________ + tip.

Caudal row immediately behind the Cloaca = C-_____. **

Caudal inclusions absent ____. M-V ____, V-L ____, L ____.

Ventral-caudal rows from Cloaca to Unity = __________.

# of Ventral scales from Cloaca to Gular Collar =

left _______. right _______. average __________.

Transverse count = _________ in the 8th row from the Collar.

Transverse count = _________ in the 9th row from the Collar.

Transverse count = _________ in the 10th row from the Collar.

Draw one of them. _______________||_______________

#_____ ==> _______________||_______________

Draw Collar.

left || right

arm || arm

Throat count = ______, or ______, average = ________ scales.

Draw the Cloacal Oval and the transverse rows immediately anterior and posterior to it.

anterior

Mark 1st belly row that counts.

||

Number the tail row that counts.

Check same data ** above.

posterior

The last dorsal row above the back legs is ______________.

The first dorsal row behind the back legs is ______________.

X = no check = yes by ________________ XXL _____ p. 1 shorter

Osteolaemus ___

niloticus ___ Locality ________

Cataphractus ___ ________ XXL-________

4 pp. protocol; samples, much detail.

other, *Crocodylus, Mecistops, Osteolaemus* XXL _____ p. 2 shorter

PC-18 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 18

PC-17 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 17

PC-16 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 16

PC-15 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 15

PC-14 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 14

PC-13 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 13

PC-12 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 12

PC-11 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 11

PC-10 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 10

PC-9 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 9

PC-8 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 8

PC-7 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 7

PC-6 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 6

PC-5 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 5

PC-4 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 4

PC-3 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 3

PC-2 |__|__|__|__|__||__|__|__|__|__|__| _____/_____ 2

PC-1 |__|__|__|__|__||__|__|__|__|__|__|<<-- _____/_____ 1

C-1 |__|__|__|__|__||__|__|__|__|__|__|

C-2 |__|__|__|__|__||__|__|__|__|__|__|

mm = 2 contiguous. x = free dorsal. blank = full scale-width missing.

o = lateral floater. Take some notes on the hindlegs and feet.

Scales above the heel smooth __ low-keeled __ sawtooth __.

||____________________||

____\ /____ PC-27 = _____//_____ PO

\/ 24-25-26 = _______________

22&23 |__|__||__|__| _____/_____ 22-23

20 & 21 |__|__||__|__| _____/_____ 20-21

Skin here? ---------------- yes ___ no ___.

19 |__|__||__|__| _____/_____ 19

Skin here? ----------------- yes ___ no ___.

__|__|__|__||__|__|__|__ PC-______.

X = no check = yes by ________________ XXL _____ p. 2 shorter other, *Crocodylus, Mecistops, Osteolaemus* XXL ____ p. 3 shorter

Is PC-22&23 longer than PC-20&21 ____. ||______________||

Is PC-20&21 longer than PC 22&23 ____.

Is skin between 20&21 and PC-19 ____.

Is skin between PC-19 and Thorax ____.

Are Nuchals anomolous ____.

__|__|__||__|__|__ PC-23 ____ / ____

__|__|__||__|__|__ PC-23 ____ / ____

_|__|__||__|__|_ PC-22 ____ / ____

__|__||__|__ PC-20 ____ / ____

_|__||__|_ PC-19 ____ / ____

__|__|__||__|__|__ = PC-______, or

not known ____. Mark midline skin on drawing.

date ______ / ______ / ______. Whole ______ ______.
day month year alive dead

Part only? Explain ______________________________.

Locality ______________________________

______________________________.

mm or cm SIZE = ______________ 9W

Snout width immediately before the eyes = __________ 4-4

Maximum head width at posterior jaw joint = __________ 1-1

Midline snout length to 4-4 line estimated = __________ 3-4M

Diagonal snout length to eye (skin) = __________ 3-5S

inside orbit or (skull) = __________ 3-5 of Kälin should be longer

Head length along midline to level of 9W = __________ 3-9

Total head length along dorsal midline = __________ 3-6

If clean skull, total head length to condyle = __________ 3-2

Neck & body from head (6) to S/C juncture __________ mm cm

Double-crested length from S/C jct. to Unity = __________

SCC length from Unity to tip = __________. Damaged __________

Measured above the animal, total length = __________ mm cm

Measured along flat ground marked, total length = __________

note any change in meas. units by __________ XXL ____ p. 3 shorter

Second-side

date ______________
day/month/year

other, *Crocodylus, Mecistops, Osteolaemus* XXL ____ p. 4 shorter

Snout-Vent nose tip to anterior end of Cloaca __________

Snout-Vent nose tip to posterior end of Cloaca __________

Snout-Vent lower-jaw tip to ant. end of Cloaca __________

Snout-Vent lower-jaw tip to post. end of Cloaca __________

Tail length Cloaca to Unity = __________.

Tail length Cloaca to end = __________. Cloaca length ________

Symphysis length ________ Overhang length ________ est.

Mandibular symphysis extends to the level of the ________ th

tooth, when viewed from below. With skin? yes ____ no ____.

Mandibular symphysis extends to level of the ________ th

tooth when viewed from above. With skin? yes ____ no ____.

Number of mandibular teeth. ________ ________. ventral pore(s)

Number of premaxillary teeth ________ ________. ☐ draw yes/no

Number of maxillary teeth ________ ________.

Color of tongue ______________ Color of eye ______________

Color of dorsal head ________. Color of neck & body ________

Color of tail ______________ Count bands on tail ________.

Color of belly ______________________________.

Draw nostril-bump.

Draw whole eyelid in place.

Note if 1st maxillary teeth
poke through premax bones.
If so, draw holes from above.

If cleaned skull,
draw external narial aperture,
and draw eyelid-bones in place.

Is the septum complete? yes ____ no ____.

If no, then what percentage is ossified? __________ %

percentage from nasal bones = __________ %

percentage from premaxillaries = __________ %

Weight of whole animal = ______________ grams kilograms

Sex of animal = male ____ female ____ Certainty ______ %

note any change in meas. units by __________ XXL ____ p. 4 shorter

XXL-____________________

PC-1 located by pelvis ____, femurs ____, width _____.

Double-crested caudals = _________ to but not including unity.

Thoracics continuous anteriorly to PC- ______.

Thoracics continuous with cervicals = yes ____, ? ___, no ____.

Neck armor = ______//______ PO's
____ // ____

Nuchals in _______ transverse rows, of _____ / ______.
_____ / ______
PC-19 ____ / ____

Draw other than *Crocodylus* model.

Belly skin collar to vent = _________ or _________.

First row behind the cloaca is C- _______.

Ventral
Pore(s)
draw
Yes / no

First row behind the back legs is C-_______.

Caudal inclusions ventral ____, lateral ____,
ventro-lateral ________, or absent ________.

3K-6K = __________ mm cm Width at 6K = __________.

3K to front of ears midline = _______, where SIZE = _________.