

**Some Critical Notes on the
Dissertation
*Analysis of the Rubbing Behaviour
of Psammophiids: A
Methodological Approach* by
Stéphanie De Pury
(De Pury 2011)**



*Open for discussion & improvement,
initiated by*

*Ton Steehouder and Michel-François
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Introduction

In December 2010 Stéphanie De Pury obtained her doctor degree at the Rheinischen Friedrich-Wilhelms-University of Bonn with a dissertation on the rubbing behaviour of Psammophiid snakes. First promotor was the well known herpetologist Prof. Dr. Wolfgang Böhme, second promotor Prof. Dr. Gerhard von der Emde. The dissertation was published in 2011.

In this publication we evaluate some aspects of this dissertation. Does it give readers a reliable picture of the rubbing behaviour of Psammophiids, and does it present a plausible explanation or interpretation of this behaviour?

Our main conclusions are that the answers to these questions are negative. The author made serious methodological failures and the design of the research was inappropriate. She neglects data and plausible explanations presented by former authors.

We invite our readers to add to this publication comments and supplements that can eventually be incorporated in future improved editions, readers thus becoming co-authors.

Readers are also invited to propose improvements in style and grammar, as the authors are not native speakers (and writers) of English.

Summary of the dissertation

The object of this dissertation is to analyse the behavioural and functional aspects of the rubbing behaviour of Psammophiids, which - briefly described - consists in a series of movements by which the snake applies a thin trace of a nasal secretion on the ventral side of its body.

After a brief introduction to the Psammophiids, the author zooms in on this rubbing behaviour, of which she very (too) briefly summarises the available literature. There are rudely two 'explanations' of the rubbing behaviour: an older speculation that it would be of use in the prevention of water loss, and a more recent that it is a preliminary act to marking behaviour, used to mark hunting routes, territories, places and conspecifics.

The author then formulates 5 'working hypotheses':

- a) the scale ultrastructure of psammophiids differs from those of other snakes;
- b) the composition of the nasal gland secretion of *Psammophis mossambicus* and *Scutophis moilensis* is similar to the one of *Malpolon monspessulanus*;
- c) rubbing behaviour is not a marking behaviour;
- d) rubbing behaviour depends on external factors as temperature;
- e) morphological divergences support the differentiation of the genera *Malpolon* and *Scutophis*."

The hypotheses are clarified very briefly.

To test these hypotheses, 17 snakes of 8 species (5 genera) are observed in terraria cages, by use of cameras. The findings are analysed.

Parts of shed skins and samples of preserved specimens of psammophiids and control-taxons were analysed by scanning electron microscopy. No pores could be identified on the median dorsal surface scales. Four different 'patterns were found in the microstructure of the dorsal scale surface.

The nasal secretion of two snakes (2 species) was scraped off the surface and analysed by use of gas chromatography (hypothesis b). There were no clear conclusions to be drawn from this analysis.

For hypothesis e the chest region of *Scutophis moilensis* and *Malpolon monspessulanus* was analysed with X-rays. The ribs in that section were clearly longer in *S. moilensis* than in *M. monspessulanus*.

The key hypothesis is c. The tests and experiments in the study did not confirm the vision that rubbing behaviour serves marking in any way (however: see in the following our remarks).

As far as hypotheses d is concerned: the over all rubbing frequency seemed to increase with increasing temperature, but it was not possible to determine a significant correlation for the individual species.

In the end, none of the hypotheses a-d could be confirmed. Hypothesis e was confirmed. The author states that De Haan 2003b wrote that parietal pits were absent from *Scutophis moilensis*, but that she found pits not only on the parietal scales but also on the frontal one.

There is an appendix with some observations about the rubbing frequency before and after shedding, about observed breeding behaviour in *Psammophylax acutus acutus*, about observed curious body movements (undulating movements with the forepart of the body), and about spreading of ribs and nasty smelling in *P. acutus acutus*.

Our findings

We have some critical remarks about the described dissertation. The main points are:

1. It is not always clear what led the author to the formulation of her hypotheses;
2. Some hypotheses are formulated clumsily and different from what appears to be the real hypothesis later on;
3. It is not explained why hypothesis e appears in a dissertation about the rubbing behaviour of psammophiids;
4. The experimental design is sometimes poor;
5. Argumentation is often unclear or even contradictory;
6. No justice has been done to former studies about the main subject of this dissertation;
7. The conclusions in this dissertation go way beyond the presented data.

1 It is not always clear what led the author to the formulation of her hypotheses

Hypothesis c: "rubbing behaviour is not a marking behaviour"

We quote: 'The decisive argument against the marking of a territory is given by juvenile psammophiids, also performing RB after the first shedding (BRANDSTÄTTER, 1996), a period of time certainly too short for the snake to have founded a territory.' This is the only motivation she gives for her principal working hypothesis.

We don't think this is a relevant argument at all as it seems to be based on the in our opinion false idea that the rubbing behaviour of these snakes is some kind of *intentional* activity, only shown in (in our human eye) relevant situations. Animals are often acting instinctively, even if at a certain age or in a certain situation the act seems to be completely irrelevant in our human opinion. Even when mature, the rubbing snake will very likely 'have no idea' why it is doing this. It just does. Juveniles often behave like adults, though their acts are not 'useful' yet.

Another point is that the argument for this argumentation seems to suppose that chemical marking behaviour serves *only* the marking of a territory. There could, however, be other functions (too) as is stated elsewhere in this dissertation too.

And then, another objection can be made. The author refers in her statement above cited to BRANDSTÄTTER (1996), but it is not at all clear on what number of observations Brandstätter based his statements about the rubbing of juvenile specimens. In his dissertation (1995) on which the 1996 book is based, no further details are mentioned. Is it true that juveniles show rubbing behaviour in the same frequency and at similar occasions as adults? In the dissertation of De Pury only adult specimens were involved. One of us (TS) observed (and filmed) RB of rather young/small specimens of *P. schokari* (age unknown, wild caught) and *P. sibilans* (about 8 months old), but it is not at all clear at what age or size these snakes are no longer juveniles and/or start marking a (supposed) territory, apart from any other 'reason' for rubbing.

We conclude: the introduction of hypothesis c ('Rubbing behaviour is not a marking behaviour') is clearly not based on valid argumentation, for instance based on observation or profound study of literature. The only given argumentation is, as we said, in our opinion irrelevant.

2 Some hypotheses are formulated clumsily and differ from what appears to be the real hypothesis later on.

The first hypothesis (a) is: 'The scale ultrastructure of psammophiids differs from those of other snakes' (p. 18).

This is a very wide formulation. In her explanation the author formulates the real, more concrete hypothesis: 'The working hypothesis was that psammophiids do not have porous structure on their scales and therefore have to protect their skin by another way – by smearing of the nasal gland secretion.' Why on earth would one formulate an 'official' hypothesis that is clearly not the hypothesis that was studied?

And this real hypothesis sounds very odd: if there is no porous structure, why would one suppose loss of water through the skin? And if there is no permeating of water through the skin, why would there be any need of protection against it?

A similar objection has to be made to the second hypothesis (b): 'the composition of the nasal gland secretion of the *Psammophis mossambicus* and *Scutophis moilensis* is similar to the one of *Malpolon monspessulanus*.' As we shall point out more in detail later on, this hypothesis is far too vague. What is *similar*? Also *wet*? The author corrects this hypothesis too: 'the working hypothesis is that the secretion would contain lipids in both species'. But then: what kinds of lipids, with what function(s)?

Hypothesis c is a troublesome hypothesis, as it is negatively formulated.

The negative hypothesis as it is, could only be proven correct by finding evidence that RB has no effect at all, in any way, on the behaviour of members of the same species or (food)competitors of other species. Such an evidence is very hard to find. Even a possible evidence that RB has other effects that are not related to marking in any way, for instance an effect on the water retaining of the skin, would be no proof for the correctness of the hypothesis: both effects could be the case (as is admitted in this dissertation).

This hypothesis is a serious mistake. It would have been more adequate if the author would have formulated another hypothesis, for instance: 'RB is effective as a means to reduce loss of water through the skin'. In that case this study wouldn't have found proof for that either. What is more: the author didn't even make a serious try for such a proof.

The last hypothesis (e): 'Morphological divergences support the differentiation of the genera *Malpolon* and *Scutophis*' does not belong in this dissertation as we already pointed out above.

All by all the working hypotheses of this dissertation are poorly chosen and formulated.

3 It is not explained why hypothesis e appears in a dissertation about the rubbing behaviour of psammophiids;

Very interested in the author's research into and view upon the Rubbing Behaviour of Psammophiids, we eagerly started reading her dissertation. However, after some scanning of the content, we were also puzzled by the presence of large parts about interesting morphological differences between *Malpolon* sp. and *Rhagheris* (*Scutophis*, *Malpolon*) *moilensis*. Of course, we wished to find out what this could have to do with the rubbing behaviour. The dissertation gives no answer to that question, and we ended to suppose that the morphology item was added as a sub-subject because the material

was available from another study that would be published soon as a hardcopy in Böhme & De Pury (2011). It would have been more suitable if this section would have been placed among the Addenda.

4 The experimental design is sometimes poor

Hypothesis d supposes a relation between rubbing behaviour and temperature. In the study this is focused on the loss of water caused by heat. One would suppose that relative humidity plays an important role in this hypothetical relationship.

In par. 4.3.3 the author indicates that the relative humidity is not intentionally varied in the research, but it was measured at the beginning and at the end of the experiment, and no significant relation between relative humidity and rubbing behaviour was found.

For future investigation, it would by the way be very interesting to find out if the frequency of RB is also influenced by the quality and the composition of the substrate on which the animal moves.

There is more doubt about the chosen experiments in studying the effects of the rubbing behaviour. For instance, the use of the glass plate that was placed in the middle of the terrarium to determine whether there would be a visible residue of the nasal secretion after the snake had been crawling over it, assumes that the amount of secretion needed for marking would be visible at all. It is however rather plausible that only extremely small particles of the substance are needed in an extremely small quantity. Cf. a dog that is tracking a person that ran from one place to another: it would be useless to look for visible particles on which the dog bases his tracking.

De Haan calls the rubbing behaviour a *preliminary act*: only after the secretion is applied, it is possible to mark traces etc. by crawling over them and leaving small particles scraped off from the belly.

Secondly, the use of blotting paper stuck to the wall of the terrarium is based on the assumption that the often observed (e.g. DE HAAN 1999) appliance of nasal secretion against glass panels as seen with *Malpolon*, is independent of the very fact that these glass panels are *windows*, and the assumption that the same snakes would apply a comparable quantity of nasal secretion on other vertical surfaces too.

Malpolon sometimes rubs the front window of his terrarium. We have seen this in *Psammophis schokari* too (though seldom). A plausible hypothesis would be that these snakes, having a very good visual acuity, are very capable to observe the exterior environment to his cage and therefore identify some distinct points usable eventually for a future special orientation. Or, one could suggest that the animals try to press *through* the window trying to continue their way to some elaborate hunting field that they observe.

The terrariums of one of us (MFH) are inter-connected by wooden tunnels, the front side of these tunnels consists of glass but can be obscured by a wooden panel. On several occasions, he noted that when the wooden panel is on the glass, there is no nasal deposit on the glass.

Why this elaboration?

De Pury in this dissertation clearly simply assumes that the visible markings on the front glass panels are the result of an action more or less identical to the presumed marking behaviour, and that the amount of nasal secretion applied to the glass panels is comparable to that of the presumed marking traces the snake causes by crawling and scraping off the belly. On this assumption the design of this experiment was based. She seemed to assume that it would be possible to see the trace on the horizontal glass plate after the snake crawled over it, even without use of a microscope. This is almost unbelievable.

In short: the experiment designed by De Pury to investigate the marking behaviour of these animals is based on false presumptions and therefore unproductive.

In the research underlying this dissertation there was also an experiment in which was investigated whether snakes that were placed in a terrarium after another snake had been rubbing and moving in it.

There was no behaviour observed that could be influenced by the rubbing of the predecessor, whether a male or a female was involved. This is interesting, more so because an experiment still being in progress by a Swiss snake keeper gives a first indication of a completely different result. When this experiment will be published, it will be possible to try to get an answer why these effects were not seen in the experiment described in this dissertation.

On p. 81 the author states: 'The results showed that the RB frequency of the 17 snakes observed is not significantly elevated when the snake is placed into an unknown terrarium so that in this case, RB cannot be considered as being used to mark a new environment.'

A terrarium is by definition a closed place and those utilised in the experiment seem to be of limited size. It is rather impossible to draw conclusion regarding the marking of a territory or a path on a surface in a volume immediately perceptible by the animal, and this in a glance.

The design of this experiment seems to be rather poor too.

One of our strongest objections concerns the study of the micro-structure of the dorsal scales as presented in this study. The author originally planned to examine (parts) of 2 or 3 dorsal scale rows and 1 lateral scale (from the first row of scales in contact with the ventral scales), but 'Since the structure of the lateral scales was less pronounced than the one of the dorsal scale, only the dorsal scales were further analyzed' (p. 3.1). This is a capital mistake in our vision. It is clear that the rubbing action only involves part of the skin, and this part is clearly NOT the dorsum above the 3rd scale row. Rubbing of the first lateral scale rows, on the contrary, is almost always involved, so even simply the fact that these scales are 'less pronounced' diminishes any importance that could be attributed to the structure of the dorsal scales for the rubbing act.

We add to this, that the rubbing of all psammophiids involves always the ventral scales, and often (but not in all species) the first lateral scale row(s).

If the objective of the rubbing act would be to apply some secretion on all of the skin (to prevent water loss, for instance), one would assume that the rubbing action would involve the dorsal as well as the ventral scales. And supposed that the micro-structure of the ~~dorsal~~ scales would serve to retain and even spread the secretion (by means of an unproven capillary action) as De Pury supposes ¹, it would be obvious to pay attention to the micro-structure of the *ventral* scales, as these are the main target of the rubbing act. But these ventral scales were strangely enough not object of her study. The lateral scales were left out of the study because their structure was less pronounced than that of the dorsal scales. It is not explained why this difference is not considered meaningful in the context of this study. If the author would be of the opinion that the differences between dorsal, lateral and ventral scale structure are unimportant, we must refer to BRANDSTÄTTER 1995: "An den Flanken ist die gleiche Struktur weniger deutlich ausgeprägt, auf der Unterseite verschwindet sie fast ganz oder weicht einem schwach ausgeprägten Leistensystem, das durchaus als Abwandlung aus der arttypischen Struktur entstanden sein kann" (BRANDSTÄTTER 1995, Band 2, p. 338). For readers that don't understand German: on the ventral scales there is almost no structure present, or only very weak.

Studying the mid-*dorsal* scales (and not the *ventral*) and deliberately leaving out the *lateral* scales, as De Pury did, is in our vision a capital (and unbelievable) mistake.

All the pages dedicated to this part of the research are a waste of time and paper.

Speaking about statistics: the vision of the author of this dissertation is, that a behavioural study has to be based on statistics, concerning a defined number of individuals in a controlled situation. This dissertation proves the restrictions of this vision. In this study there has not been research on animals in their natural environment. Admittedly, it is almost impossible to study this rubbing behaviour in the wild, and it is virtually impossible to create a controlled environment in which all circumstances are kept in hand. The method used by De Haan, consisting in placing individuals in very large open-air

¹ Ironic is the following: the author rejects De Haan's opinion that the animals mark each other with the secretion, but would precisely her theory about the function of the micro-structure of the dorsal scales not endorse De Haan's opinion?

terrariums, recreating genuine natural biotope, seems to us an important advantage in this kind of observation.

5 Argumentation is often unclear or even contradictory

Then there is the question of the supposed protection against loss of water.

We don't see in this study any indication that a larger amount of protection against loss of water than is found in other snakes, would be useful or desirable for the studied species. On the contrary: the author herself states (in par. 4), based on study of literature, that these snakes have a sufficient and efficient protection against loss of water.

After a rather chaotic survey of the question of pores, the author concludes in par. 4.1 that no pores could be found in the skin through which e.g. lipids could pass. The same, though not explicitly mentioned, is likely to apply to water, and if/since there are no pores through which water could evaporate, and if/since studies done with scale-less snakes showed that even these snakes are optimally protected against desiccation, then we cannot see why the author still remains convinced that the rubbing act serves to protect against desiccation.

'Lipids have to be extruded by the skin to play a role against desiccation', she writes. Why would that be so? Wouldn't it be sufficient if lipids *in* the skin would act as a protective substance?

Apart from this, since it remains unclear what the precise nature is of the lipids that are applied while rubbing, we would like to know why she so strongly believes in their water-retaining function, when externally applied. She states that the applied substance seemed to be water-repellent and that this is an argument for their function in prevention of water loss. We think this is not very conclusive: butter is also water-repellent, but it is not its main function to repel water. Furthermore, the water repellent quality of the nasal secretion is not really studied in this dissertation. It could e.g. very well be that they are only water repellent during a short time.

Another point is that the author repeatedly refers to literature in which is spoken about lipids that have a pheromonal function (e.g. par. 4.2), but in the end she seems to ignore all these indications of a function of rubbing that is far more likely, and well documented in the studies of De Haan and Cluchier.

6 No justice has been done to former studies about the main subject of this dissertation

The author writes: 'Until now, despite its uniqueness among snakes, RB [= rubbing behaviour] has never been the subject of behavioural studies.' (p. 17). However, C.C de Haan has been studying the rubbing behaviour and written about it in a number of publications (e.g. DE HAAN 1982, 1999, 2003, 2006) which nevertheless are mentioned in the reference list of De Pury's dissertation and cited, though seldom correctly, along with other authors.

Further on we read: "The focus of the present study is set on a detailed analysis of this RB of psammophiids, to determine under which condition it is performed and for which purpose." What, in this respect, would be the main difference between De Haan's studies and this dissertation? One of us (TS) asked the author in an e-mail this question, and her answer was that behavioural studies should be based on statistics, and that "*De Haan has never used statistics, never used a defined number of individuals. Therefore his studies cannot be considered as behavioural studies but only as observations*" (DE PURY, *sic in litt.*).

Stubborn as we are, we don't think this is a valid argument for not considering De Haan's elaborate publications about this subject the outcome of serious behavioural studies. Admittedly, he did not use many statistics, but that is no conclusive argument. It is after all a matter of fashion and choice of subject as far as scientific publications are concerned.

It is an important fact that De Haan's observations are based on quite a lot more individual specimens than are used in this dissertation. Besides, they were not only his own observations, but he also refers to observations of a variety of other observants.

Admittedly, this dissertation adds statistics, but still for a very small number of specimens, hardly enough to get valid conclusions. Furthermore, these data only concern animals in captivity, and in a limited space, only assigned to them for a short period. The validity of any conclusion about their behaviour based on these data is thus very limited.

7 The conclusions in this dissertation go way beyond the presented data

The relevant statistic data in this dissertation concern mainly the way the animals rub, how often they do it and when they do it. As far as we can see, these data are supported by observations from De Haan a.o. and can easily be verified and illustrated by looking at the videos others than De Pury placed on Youtube (see e.g. <http://www.psammophis.net>). This is not the problem. The problem is, that the data De Pury collected about the rubbing behaviour (the core of the dissertation) do not support in any way the bold 'conclusions' she ventures to draw about the 'meaning' of the rubbing behaviour of psammophiids. Her *description* of the behaviour including their statistical processing, doesn't give any clue to its *meaning*. All explanations De Pury gives for that behaviour are very far fetched hypothetical and/or based on (mis)interpretations.

Let us go back to the supposed relation between temperature and rubbing behaviour. In par.3.3.3 the author concludes a statistical dependency of temperature and frequency of RB. Yet, it seems very hard to draw any further conclusions from these data. For instance: in 2 specimens of *P. schokari* there was a dependency, in 2 other specimens however there was not. Therefore, it seems rather premature to conclude, as the author does in par. 4.3.3, that in species adapted to heat, as *P. schokari*, a dramatic increase in temperature does not lead to more frequent rubbing. Not enough data, not enough logic.

On p. 81 there is a puzzling remark: 'The traces reappeared exactly seven days after removal'. Is this one unique observation? It is not clear either, what importance the author wants to give to this observation. In no way can we confirm this behaviour for *M. m.* or any other psammophiid on the basis of our years of experience.

Another intriguing statement in this study is: 'Since it is known that increasing temperature elevates the activity of the animal during the day (MORENO-RUEDA and PLEGUEZUELOS, 2007), a greater activity lead (sic) certainly the snake to sweat more, causing then a higher rate of water loss (in reference to WARBURG, 1965). To avoid then large amount of water loss, the snake would rub more frequently.'

It has never been proven that snakes do sweat, but the research in this dissertation, and its citations and references about the lack of pores in the snake's skin make sweating very unlikely as far as we can see.

Back to the statistics that are used to justify this study as a behavioural study. Statistics can be important, but only if they offer relevant information for the subject involved. In that sense, it is not so clear what the relevance is of part of the statistical analyses in this dissertation. For instance the gaschromatographic data of the nasal secretion: there is not much to conclude from them, and also it is very pitiful the author didn't collect that secretion directly from the nasal gland, which would have brought maybe more certainty about what exactly was examined. On the other hand: we understand that she did not want to damage the snakes involved in the research.

In par. 4.2 the author states that the analysis showed that the chromatograms were different between the species, and similar for individuals of a given species. That disproves the hypothesis ("the composition of the nasal gland of the *Psammophis mossambicus* and *Scutophis moilensis* is similar to the one of *Malpolon monspessulanus*"), unless the meaning of the word 'similar' must be interpreted so wide that it loses all meaning. But, as we said before, the real hypothesis is that the secretion would contain lipids in both species. Quote: "The presence of lipids in the nasal secretion of both species cannot be determined clearly by means of this GC/MS analysis"(par. 4.2). And: ... it cannot be said whether they are e.g. fatty acids or aldehydes"(par. 4.2). The fact that the author elaborately discusses

what would have to be done to get useful research results cannot compensate for the fact that there is not a single indication that her hypothesis would even be likely, and that her research simply failed to give any useful result. The hypothesis is therefore not ‘only partially [...] confirmed’ as she states, but a total failure.

On p. 86 the author philosophizes on the origin of the rubbing behaviour. There is 1 observation of a *Psammophylax acutus acutus* drinking water drops running from the flanks and back. Nobody ever noticed anything like this before in psammophiid snakes and it is only a single observation, but the author finds it possible that here the origin of the RB can be found. This kind of speculation is sometimes interesting, but only if presented as a remote possibility that could eventually be worked on.

Conclusion

This dissertation had to fail because of the clumsy hypotheses and the inappropriate design of the research. To make things worse, instead of sticking to her data, the author loses herself in formulating far fetched conclusions and vague new hypotheses. She neglects data and plausible explanations presented by former authors. It is hard to understand how this dissertation could be approved by scientists with such good reputation.

It is clear that that the *description* of behaviour doesn’t necessarily lead to *understanding* that behaviour. It has been the aim of this dissertation to ‘determine behaviourally the function of this ‘rubbing behaviour’ (section 5 of the dissertation, Summary). The description has brought some interesting details, but as far as the determining of the function is concerned, the author has been seduced to wild interpretations and elaborating on all kinds of hypotheses that are not in the least based on facts or valid argumentation.

Unfortunately, this dissertation cannot be considered as a standard or even preferred reference to the subject.

A note about English language in this dissertation (and in our text)

As is said in the introduction, the authors of these critical notes are not native speakers of English. Still, anybody can see at a glance that the English that is used in the criticised dissertation is abominable. Even we did.

The fact that English is the international language in the scientific world, presents a huge problem for all the scientists and students all over the world that are not native speakers of that language. It is hardly a consolation that the written English of native speakers is often just as bad as ours, or even worse.

If you are (for instance) a native speaker of English and consider yourself a skilled writer in that language, please feel free to suggest improvements for the language in this text.

References

Böhme, W., & De Pury, S, 2011. A note on the generic allocation of *Coluber moilensis* Reuss, 1834. (Serpentes: Psammophiidae). Salamandra, 47(May), 120-123.

Brandstätter, Frank, 1995. Eine Revision der Gattung *Psammophis* mit Berücksichtigung der Schwesterngattungen innerhalb der Tribus Psammophiini (Colubridae; Lycodontinae). dissertation Universität des Saarlandes.

De Haan, C.C., 1982. 'Description du comportement de 'frottement' et notes sur la reproduction et la fonction maxillaire de la Couleuvre de Montpellier *Malpolon monspessulanus*. Remarques comparatives avec *Malpolon moilensis* et *Psammophis* spp. Bull. Soc. Herp. France, No. 23:35-49 / Errata: No. 25:69.

De Haan, C. 1999. *Malpolon monspessulanus*. In: Böhme, W. (ed.), Handbuch der Reptilien und Amphibien Europas., pp. 661-756.. Aula-Verlag, Wiesbaden.

De Haan, C. C., 2003. Sense-organ-like parietal pits found in Psammophiini (Serpentes, Colubridae). Comptes Rendus Biologies, 326(3), 287-293. doi:10.1016/S1631-0691(03)00074-X

De Haan, C. C., 2003. Extrabuccal infralabial secretion outlets in *Dromophis*, *Mimophis* and *Psammophis* species (Serpentes, Colubridae, Psammophiini). A probable substitute for “self-rubbing” and cloacal scent gland functions, and a cue for a taxonomic account. Comptes Rendus Biologies, 326(3), 275-286. doi:10.1016/S1631-0691(03)00073-8

De Haan, C. C. & Cluchier, A. 2006. Chemical marking behaviour in the psammophiine snakes *Malpolon monspessulanus* and *Psammophis phillipsi*. Program, 212, 211-212.

De Pury, Stéphanie 2011. Analysis of the Rubbing Behaviour of Psammophiids: A Methodological Approach. Dissertation Zur Erlangung des Doktorgrades (Dr. rer. nat.) der Mathematisch-Naturwissenschaftlichen Fakultät der Rheinischen Friedrich-Wilhelms-Universität Bonn. September 2010. Erscheinungsjahr: 2011.