Entomol Gener | 19(4): 253-259 | Stuttgart 1995-04 | ISSN: 0171-8177

EGT-Nr 852 III

Comparison of Iso-enzyme Electrophoresis and Gut Content Examination for Determining the Natural Diet of the Groundbeetle Species Abax ater (Coleoptera: Carabidae)

ALAIN WALRANT & MICHEL LOREAU

Received: 1993-10-06 / 1994-09-09 Accepted: 1994-09-19

WALRANT A & LOREAU M [Dep Animal Biol, Free Univ Brussels, B-1050 Brussels, Belgium]: **Comparison of Iso-enzyme Electrophoresis and Gut Content Examination for Determining the Natural Diet of the Groundbeetle Species Abax ater (Coleoptera: Carabidae).**- Entomol Gener 19(4): 253-259; Stuttgart 1995. --- [Note].

A comparative study between iso-enzyme electrophoresis and gut content examination under the microscope was conducted to assess the natural diet of the groundbeetle species *Abax ater* Villers 1789. The results of the 2 methods were often different: (a) They did not always detect meals in the same individuals; their detection power (ability to reveal a meal), however, was similar. (b) The microscopic method had a distinctly higher identification power (ability to identify the prey detected) than had electrophoresis. On the other hand, the precision of the identification was often better in the electrophoretic method. Despite these differences, the number of contradictory identifications was very low. It is concluded that iso-enzyme electrophoresis is a promising method for diet analysis more especially in predators which are more specialized than *Abax ater*, and which do not present multiple predation.

Key words: Carabidae - feeding - iso-enzyme electrophoresis - gut content examination - multiple predation

1 Introduction

By their abundance and diversity, carabid beetles play an important role as polyphagous predators of primary consumers at the soil level. As a result, their feeding habits have been the subject of great interest [HENGEVELD 1980a]. Because of their often nocturnal nature, their great mobility and their activity partly within the litter layer, however, a quantitative study of their natural diet by direct observation is impractical. This natural diet therefore has been studied through indirect methods, in particular gut content examination under the microscope [DAVIES 1953, ANDERSON 1972, LUFF 1974, HENGEVELD 1980b, LOREAU 1983a, 1983b]. This method, however, cannot be applied to larvae, or to imagines of some genera, because of their pre-oral digestion.

0171-8177/95/0019-0253 $ 1.75

A number of other methods have been used [SUNDERLAND 1987: review], in particular serological methods [BOREHAM & OHIAGU 1978]. The latter, which require the preparation of specific antibodies for each prey species, have been mainly used to identify the predators feeding on a particular prey and to quantify predation on this prey. Iso-enzyme electrophoresis [MURRAY & SOLOMON 1978] seems a promising alternative or complementary method to identify the range of prey eaten by a particular predator [SUNDERLAND 1987]. It has been applied successfully to investigate the diet of several invertebrates [GILLER 1982, 1984, 1986, DICKE & JONG 1988] as well as vertebrates [WALTER & O'NEIL 1986], and was used by SCHELVIS & SIEPEL [1988] to study the feeding habits of 2 ground-beetle larvae.

However, results have been obtained so far using a single technique. There has been no attempt to compare the 2 methods, and thus to assess the efficiency of electrophoresis. The goal of the present contribution is to fill this gap through a comparative study of the diet of imagines of the groundbeetle species *Abax ater* Villers 1789, using the 2 techniques simultaneously though independently. *Abax ater* was chosen both because it is a very common species in European woodlands and because its diet was known in great detail by gut content examination and food preference experiments from previous works [LOREAU 1983a, 1984]. For this comparison the same techniques were used as in previous studies; in particular, polyacrilamide gels were stained for proteins with esterase activity following electrophoresis [MURRAY & SOLOMON 1978, GILLER 1982, 1984, 1986, SCHELVIS & SIEPEL 1988].

2 Material and methods

The beetles were collected using live pitfall traps [diameter 9 cm, height 15 cm] in a beechwood at Lembeek, Belgium, in late June 1990. To minimize their residence time in the traps, the latter were open in the evening and emptied the following morning. The prey needed to provide reference electrophoretic banding patterns were collected in the same pitfall traps and by Berleze extraction from soil samples.

To obtain reference electrophoretic banding patterns of the various prey, *Abax ater* individuals were placed in Petri dishes containing a moist paper. They were starved 2 days at about 20 °C. This period of time was found to be sufficient for a gut clearance; electrophoretic analysis of individuals after this period revealed only the characteristic bands of *A. ater*. The beetles were then provided with a known prey during one day. Those individuals which had eaten were then killed in liquid nitrogen and preserved by freezing at - 30 °C until their later analysis. Freezing does not alter results of electrophoresis [LISTER et al 1987]. The beetles sampled for analysis of their diet were killed and preserved in the same way immediately after being collected in the traps.

To allow analysis of each individual using both methods simultaneously, the following procedure was devised. After dissection, the content of the whole gut was macerated in 3 ml gel buffer, then centrifuged at 2500 revolutions per minute during 5 min. The liquid formed the sample for the electrophoretic method, while the solid residue formed the sample for the method of examination under the microscope, hereafter referred to as the microscopic method. This procedure was found to give good results for reference individuals fed in the laboratory, with both the microscopic method (solid remains alone can be used for this method, and are not altered by this procedure) and the electrophoretic method (the quantity of 3 ml to macerate the gut was found to be the best compromise between too low a concentration for prey detection and too high a concentration for gel legibility). The solid residue was filtered on a Millipore filter, dried and mounted on a microscopic slide following the method described in LOREAU [1983a]. It was identified under the microscope as in LOREAU [1983a], by comparison with reference slides and following a rule of parcimony, that is, only those remains which are not secondary constituents in the main prey were counted.

Electrophoretic gels were obtained using a Gradient Former (firm Bio-Rad) by progressive mixing of 5% and 10% acrylamide solutions. Electrophoresis was carried out during 3 hours under standardized electric conditions (400 V, 75 mA, 50 W) using a Protean X II migration tank and a 500/1000 Power Supply (firm Bio-Rad). The composition of the gel buffer was: 1.25 g boric acid, 0.25 g EDTA, 2.5 g TRIS, 0.5 ml Triton X-100 and 250 ml water; that of the tank buffer was: 7.5g boric acid, 1.5 g EDTA, 15 g TRIS and 1.5 l water. Esterase bands were detected by immersion of the gels in a solution of 0.125 g α-naphtylacetate, 0.125 g β-naphtylacetate and 0.075 g fast blue RR salt with a phosphate buffer (14.80 g $NaH_2PO_4.2H_2O$, 2.68 g $Na_2HPO_4.2H_2O$, 500 ml water), during 15 h at 15 °C in the dark. This duration of 15 h was found from preliminary trials to provide the best band resolution. Gels were then fixed during 1 h in a 7% acetic acid solution, and later preserved in a solution of 300 ml ethanol, 100 ml 95% acetic acid and 100 ml glycerine with 500 ml water. Esterase bands were analysed using an optical scanner coupled to a computer; this allowed translation of the banding patterns into graphs of optical density as a function of migration distance in the gel.

Reference gels each contained the banding patterns of a control (gut of a starved *A. ater*), of a prey, and of the gut content of an individual that had eaten this prey. Gels intended for diet analysis contained the banding patterns of a control and of individuals to be analysed. The identification of the prey eaten was performed by comparison with reference gels using the scanner.

To make the comparison as objective as possible, the same gut contents were analysed by the 2 methods independently: the first author used the electrophoretic method, while the second used the microscopic method; the results were not communicated to the other author until the end of the experiment.

3 Results

57 reference gels were made containing the banding patterns of the main potential prey of *A. ater* and of the most abundant organisms present in the pitfall traps and in the soil samples at the time when the beetles were collected (Tab 1). A total of 90 *A. ater* were analysed by the 2 methods, but electrophoresis failed to provide results for 5 individuals. Thus the results obtained by microscopic examination for those 5 individuals were also eliminated below.

The main prey groups were identified by both methods, but in different proportions and with different efficiencies (Tab 1). A detailed comparison of the pairs of results obtained by the 2 methods, rarely showed contradictory results (different prey identified by the 2 methods) but the type of information obtained differed in many cases (Tab 2).

To compare the efficiency of the 2 methods, 2 aspects were distinguished: the detection power of a method, defined as its ability to reveal a meal (non-empty gut), and its identification power, defined as its ability to identify the prey detected.

Frequently one method does not detect a meal while the other does (Tab 2). After elimination of the 15 individuals which were found to have an empty gut by both methods and for which it was assumed that they really had not eaten, the detection power was calculated as the proportion of the detected meals in the other 70 individuals. This amounted to 87% in the electrophoretic method and 83% in the microscopic method, and thus there was no significant difference between the detection power of the 2 methods ($\chi^2 = 0.50$, 1 d.f., $P > 0.6$).

On the other hand, the identification power, as measured by the proportion of identified or partly identified meals, was significantly higher in the microscopic method than in the electrophoretic method (Tab 3: $\chi^2 = 16.77$, 2 d.f., $P < 0.001$). This also appears in the much higher number of prey identified by microscopic examination (Tab 1). The precision of the identification, however, was generally better in the electrophoretic method (Tab 1).

Tab 1: Numbers of reference gels (**R**), and numbers of individuals of *Abax ater* Villers 1789 [Coleoptera: Carabidae] found to have fed on the various prey as identified by electrophoresis (**E**) and microscopic examination (**M**).- **NFI** not further identified. Note that one individual can feed on several prey; thus the numbers in columns E and M do not add to give numbers of gut contents as in Tab 2 and 3.

Prey		R	E	M
Annelida	Lumbricidae	13	4	5
	Enchytraeidae	1		
Mollusca	*Oxychilus* sp.	2		
	Discus rotundatus	1	1	
	Arion sp.	2	1	4
	Milax sp.	2		
Acari				2
Opiliones		2	2	
Araneae	NFI			15
	Tegenaria sp.	4	1	
	Florina sp.	1	1	
Chilopoda	NFI			10
	Cryptops sp.	3	3	
	Lithobius sp.	1		
	Geophilus sp.	1		
	Bothriogaster sp.	1		
Diplopoda	*Polydesmus* sp.	1		
Crustacea	*Philoscia* sp.	1		
Collembola		3		1
Hemiptera	*Drymus brunneus*	1		
Neuroptera	*Chrysopa vulgaris*	1		
Trichoptera	*Enoicycla pusilla* (larvae)	2		2
Lepidoptera	Psychidae (larvae)	2	1	3
	Noctuidae (larvae)			3
	Nematocera (imagines)			2
Diptera	Brachycera (imagines)			2
	(larvae)	3		
	Curculionidae NFI			35
Coleoptera	*Polydrosus* sp.	5	19	
	Trachyphloeus sp.	2	3	
	Peritelus sp.	2	1	
	Carabidae (larva)			1
	Staphylinidae (larva)			1
Total		57	37	86

4 Discussion

It is first worth comparing the present results on the natural diet of *A. ater* with those obtained previously over longer periods [LOREAU 1983a]. In the present study, unusually high proportions of prey that are generally avoided because of their hard cuticle or their predatory behaviour (weevils, spiders, centipedes) were found, as well as unusually low proportions of earthworms and molluscs. These differences correspond to dif-

ferences in the relative abundances of these prey groups at the time when the beetles were collected, which are themselves explained by the relative dryness prevailing at that time. These results thus confirm the especially opportunistic feeding behaviour of *A. ater*, whose diet can undergo wide seasonal fluctuations [LOREAU 1983a].

Tab 2: Direct comparison between the analyses of the same gut contents of *Abax ater* Villers 1789 [Coleoptera: Carabidae] by 2 methods (numbers of gut contents in the various categories).- **I** identified; **N** not identified; **V** empty; **E** by electrophoresis; **M** by microscopic examination. Definition of categories: **(a)** Identical: results strictly identical by the 2 methods (same prey identified, gut found empty, or gut content not identified). **(b)** Partly identical: several prey detected; one of them identified by both methods, and at least one of them not detected or identified by one method (ex: IE/IM + IM: one prey identified by both methods + one or several other prey identified by microscopic examination but not by electrophoresis). **(c)** Different: different types of results by the 2 methods (ex: NE/IM: prey detected but not identified by eletrophoresis; one or several prey identified by microscopic examination). **(d)** Contradictory: at least one prey identified by each method, but identifications different.

Results of the 2 methods		**Nr**
Identical	IE / IM	11
	VE / VM	15
	NE / NM	3
Partly identical	IE / IM + IM	9
	IE / IM + NE	2
	IE / IM + NM	1
Different	NE / IM	19
	VE / IM	8
	IE / VM	10
	VE / NM	1
	NE / VM	2
	IE / NM	2
Contradictory	IE ≠ IM	2
Total		**85**

Tab 3: Comparison of the powers of 2 methods for the identification of the gut content of *Abax ater* Villers 1789 [Coleoptera:Carabidae].- For each method, the numbers of gut contents are given in which prey were detected but not necessarily identified (non-empty guts); according to results shown in Tab 2].

	Electrophoresis	**Microscopy**
Identified	25	44
Partly identified	12	8
Not identified	24	6
Total	**61**	**58**

The comparative study of the electrophoretic and microscopic methods showed that their results were often different. There were 2 main types of differences. The first one was that the 2 methods did not always detect meals in the same individuals. This is explained by the fact that detection of a meal depends on the gut state [GILLER 1984] and the 2 methods are not sensitive to the same prey remains. Electrophoresis detects remains in the liquid phase, while microscopic examination detects remains in the solid

phase, and the progress in the digestion of the 2 phases may not always be identical. A similar difference was found by SUNDERLAND et al [1987] in a comparison between serology and microscopic examination to assess cereal aphid consumption. Despite this difference, neither of the 2 methods was found to detect meals better than the other.

The second main type of differences was the distinctly higher identification power of the microscopic method. A relatively high proportion of meals was not identified using electrophoresis (39% vs 10% using microscopic examination). Several factors can explain these shortcomings of the electrophoretic method.

(a) Esterases are polymorphic, and thus a single species can present several different banding patterns [GILLER 1984, SCHELVIS & SIEPEL 1988]. In particular, it is sometimes difficult to identify the bands of a prey when these are in a zone of polymorphism of the predator. However, this difficulty can often be overcome due to the presence of other bands allowing identification of the prey.

(b) In the case of such a broadly generalist predator as *A. ater* [LOREAU 1983a, 1984], the number of reference gels becomes an important limiting factor. Several prey types which were revealed by microscopic examination (Tab 1: Noctuidea larvae, Diptera imagines, Coleoptera larvae) were not found in the pitfall and soil samples collected to establish reference gels. Since each banding pattern is species-specific and not every prey species can be collected to establish reference gels, the results of electrophoresis depend on the intensity of sampling of prey species. On the other hand, the more numerous the potential prey, the more likely a confusion in the interpretation of the observed banding patterns. The use of several types of enzymes could alleviate this problem, though at the cost of more work.

(c) The main cause for the failures of the electrophoretic method to identify a meal in the present study seemed to be multiple predation by *A. ater*. In more than half of the cases where a meal was not identified (13 out of 24 cases), feeding on several different prey types was revealed by microscopic examination. In such cases, it is often impossible to interpret the banding patterns because they can result from several different combinations of prey. This is an important intrinsic limitation of the method.

(d) Lastly, a potential cause of differences between the results of the 2 methods may also be our respective experiences of the methods (thus, the second author was experienced in the microscopic method prior to this study). This is a factor that is difficult to control; it is unlikely to explain the major differences between the results of the 2 methods, but it may have played a limited role.

On the other hand, the precision of the identification was often better in the electrophoretic method. Electrophoresis allows identification at the species level (although not all references were identified to this level), while the level of identification by microscopic examination varies depending on the available characters in the various taxonomic groups.

In spite of the differences between the results of the 2 methods, the number of contradictory results was very low. Thus the risk of an erroneous identification of a prey by either method is low.

In conclusion, iso-enzyme electrophoresis can be regarded as a promising method for diet analysis more especially in carabids or other invertebrates which are more specialized predators than is *Abax ater* and which do not present multiple predation. Microscopic examination, which is easier to carry out, should be recommended whenever it is applicable (predators without a pre-oral digestion). However, electrophoresis can then provide useful complementary results when more precise information is necessary.

5 References

ANDERSON J M [1972]: Food and feeding of Notiophilus biguttatus F. (Coleoptera: Carabidae). - Rev Ecol Biol Sol **9**: 177-184; Paris / France.

BOREHAM P F L & OHIAGU C E [1978]: The use of serology in evaluating invertebrate predator-prey relationships: a review. - Bull Entomol Res **68**: 171-194; London / UK.

DAVIES M J [1953]: The contents of the crops of some British Carabid beetles. - Ent mon Mag **89**: 18-23; Oxford / UK.

DICKE M & JONG M [1988]: Prey preference of the Phytoseiid mite Typhlodromus pyri. 2. Electrophoretic diet analysis. - Exp appl Acarol **64**: 15-26; Amsterdam / Nederland.

GILLER P S [1982]: The natural diets of waterbugs (Hemiptera-Heteroptera): electrophoresis as a potential method of analysis. - Ecol Entomol **7**: 233-237; Oxford / UK.

GILLER P S [1984]: Predator gut state and prey detectability using electrophoretic analysis of gut contents. - Ecol Entomol **9**: 157-162; Oxford / UK.

GILLER P S [1986]: The natural diet of the Notonectidae: field trials using electrophoresis. - Ecol Entomol **11**: 163-172; Oxford / UK.

HENGEVELD R [1980a]: Qualitative and quantitative aspects of the food of ground beetles (Coleoptera: Carabidae): a review. - Neth J Zool **30**: 555-563; Leiden / Nederland.

HENGEVELD R [1980b]: Polyphagy, oligophagy and food specialization in ground beetles (Coleoptera: Carabidae). - Neth J Zool **30**: 564-584; Leiden / Nederland.

LISTER A, BLOCK W & USHER M B [1987]: Description and quantification of field attack rates by predatory mites: an example using an electrophoresis method of Antarctic mites. - Oecologia **72**: 185-191; Berlin / Deutschland.

LOREAU M [1983a]: Le régime alimentaire de Abax ater Vill. (Coleoptera, Carabidae). - Acta Oecologica, Oecol Gener **4**: 253-263; Montreuil / France.

LOREAU M [1983b]: Le régime alimentaire de huit carabides (Coleoptera) communs en milieu forestier. - Acta Oecologica, Oecol Gener **4**: 253-263; Montreuil / France.

LOREAU M [1984]: Etude expérimentale de l'alimentation de Abax ater Villers, Carabus problematicus Herbst et Cychrus attenuatus Fabricius (Coleoptera, Carabidae). - Ann Soc r zool Belg **114**: 227-240; Bruxelles / Belgique.

LUFF M L [1974]: Adult and larval feeding habits of Pterostichus madidus (F.) (Coleoptera: Carabidae). - J nat Hist **8**: 403-409; London / UK.

MURRAY R A & SOLOMON M G [1978]: A rapid technique for analysing diets of invertebrate predators by electrophoresis. - Ann Appl Biol **90**: 07-10; Cambridge / UK.

SCHELVIS J & SIEPEL H [1988] Larval food spectra of Pterostichus oblongopunctatus and P. rhaeticus in the field (Coleoptera: Carabidae). - Entomol Gener **13**: 61-66; Stuttgart / Deutschland.

SUNDERLAND K D [1987]: A review of methods of quantifying invertebrate predation occurring in the field. - Acta Phytopath Entom Hung **22**: 13-34; Budapest / Magyar.

SUNDERLAND K D, CROOK N E, STACEY D L & FULLER B J [1987]: A study of feeding by polyphagous predators on cereal aphids using ELISA and gut dissection. - J Appl Ecol **24**: 907-933; Oxford / UK.

WALTER C B & O'NEIL E [1986]: Electrophoresis in the study of diets and digestive rates of seabirds. - Comp Biochem Physiol, A: Comp Physiol **84**: 763-765; London / UK.

Acknowledgements: We are grateful to H Siepel for welcoming A Walrant in his laboratory and commenting on the manuscript.

Authors' address: Alain Walrant & Professor Dr Michel Loreau, Départment de Biologie Animale, CP 160/13, Université Libre de Bruxelles, 50 av Roosevelt, B-1050 Bruxelles, Belgique. - **Present address** and address for correspondence: Professor Dr Michel Loreau, Institut d'Ecologie, Université Pierre et Marie Curie, Bât. A, Case 237, 7 quai Saint Bernard, F-75252 Paris Cedex 05, France.

DAY R & WENDLAND J: **Nationalparks in Skandinavien.**- [240 Seit, 80 Farbfot, 3 Länderkart, 210x270 mm, Hartkart.Einbd, Schutzumschl].- Publ: Leopold Stocker Vlg, Graz-Stuttgart 1991; ISBN: 3-7020-0615-X; Pr DM 68,--. ----- [EGR-Nr 2121].

Das vorliegende Werk hat im Grunde genommen nichts mit Biologie oder gar speziell mit Entomologie und eigentlich nur am Rande mit Ökologie zu tun. Es ist vielmehr ein Sachbuch und Reise-Handbuch. Als solches aber liefert es wertvolle Informationen für jeden Biologen, der in den zum Vergleich mit Mitteleuropa noch immer naturnäheren und sogar weithin noch natürlichen Bereichen nordeuropäischer Wildnis Forschungsarbeiten durchführen oder sich ganz einfach mit der dortigen Flora und Fauna und ursprünglichen Lebensgemeinschaften vertraut machen will. Ihm sei dieses gut bebilderte und und unterhaltsam geschriebene Buch zur Einstimmung und Vorbereitung wärmstens empfohlen.

***

BATTEFELD K-U (Hrgb): **Artenschutzrecht. Bedrohte Tiere und Pflanzen**: Internationale Vereinbarungen - EG-Recht - Bundesvorschriften - Ländervorschriften - Materialien. (2. verändt Aufl, Loseblattwerk in 2 PVC-Ordnern). 15. Ergänzungsliefg [160 Seit, 145 x 210 mm].- Publ: Deutscher Fachschriften-Vlg Wiesbaden / Hüthig Vlg.gem Heidelberg 1994; ISBN: 3-8114-0800-3; Pr: DM 75,50. --- [EGR-Nr 2289].

Die vorliegende Ausgabe zum Artenschutzrecht bringt wieder eine wertvolle Ergänzung zu der Vielzahl von auf EG-, Bundes- und Länderebene geltenden Vorschriften, die durch internationale Konventionen stark miteinander verflochten und damit auch für den Fachmann kaum noch überschaubar sind. Es beinhaltet die folgenden erst in jüngerer Zeit in Kraft getretenen Gesetze: (**a**) Gesetz über den Schutz der Natur und die Pflege der Landschaft (Saarländisches Naturschutzgesetz - SNG) vom 19. März 1993, (**b**) Sächsisches Gesetz über Naturschutz und Landschaftspflege (Sächsisches Naturschutzgesetz - SächsNatSchG) vom 16. Dezember 1992, (**c**) Gesetz zum Schutz der Natur (Landes-Naturschutzgesetz - LNatSchG-) in der Fassung vom 16. Juni 1993 und in Ausführung des Artikels 7 der Verfassung des Landes Schleswig-Holstein.

BRAUNS A: **Taschenbuch der Waldinsekten.** Grundriß einer terrestrischen Bestandes- und Stand- ort-Entomologie. 4. neubearbeit Aufl.- [XVIII+860 Seit, 1056 Abb davon 234 auf Farbtaf, 120x190 mm, Balacr.Hartkart.Einbd].- Publ: Gustav-Fischer-Vlg, Stuttgart-Jena 1991; ISBN: 3-437-30613-8; Pr: DM 78,--. --- [EGR-Nr 2092]

Ein Forscherleben feldentomologischer Erfahrungen spiegelt sich in diesem Werk wider. Die Tatsache, daß es innerhalb von 30 Jahren in bereits 4. Auflage erschienen ist, offenbart den wissenschaftspädagogischen Wert dieses Lehr- und Anleitungsbuches und bezeugt den regen Zuspruch, der ihm durch Studierende der Biologie und Forstwirtschaft, aber auch durch interessierte Laien und Naturfreunde zuteil geworden ist. Als Standardwerk der Eidnomie, Ethologie und Ökologie der Waldinsekten und der biozönotisch und bodenzoologisch orientierten Forstentomologie hat es längst seinen verdienten Platz im deutschsprachigen entomologischen Schrifttum gesichert. Auch die vorliegende jüngste Ausgabe hat vor allem durch die Aufnahme eines neuen Kapitels über die aktuellen Probleme des Waldsterbens wieder eine Bereicherung und Erweiterung erfahren. Auch die Aufnahme neuer Farbtafeln ist zu begrüßen. Eine Aktualisierung der Literatur ist jedoch bei der Fülle der zu behandelnden Arten und ihrer Lebensäußerungen sowie der Vielfalt ihrer Lebensräume nicht in jeder Weise gelungen. Nicht alle der nachweislich im Text berücksichtigten neueren Veröffentlichungen werden im Schriftenverzeichnis aufgeführt; andere wesentliche Befunde bleiben unerwähnt; gleiche im Text und in Bildunterschriften benannte Kategorien stimmen nicht immer überein. Trotz dieser bei einer wünschenswerten weiteren Auflage zu behebenden kleineren Mängel muß man dieses Taschenbuch aufgrund seiner informativen Beschreibungen und zeichnerischen Darstellungen immer wieder und nachdrücklich empfehlen.

A Wilhelm Steffan (Ruhr-Universität Bochum)