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The Work of FRANZ Baron NOPCSA (1877-1933): Dinosaurs, Evolution and Theoretical Tectonics

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With 2 figures and 1 table

Dinosaurier
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Systematik
Histologie
Paläobiologie
Archaeopteryx
Evolution
Orthogenese
Neolamarckismus
Biogeographie
Vulkanismus
Orogenese
Kontinentalverschiebung

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Summary

The scientific studies of FRANZ Baron NOPCSA have received only minor modern analysis, despite their relevance to early works in dinosaur paleobiology, neo-Lamarckian evolution, theoretical tectonics and paleobiogeography. NOPCSA's contemporary impact in these areas varies from progressive and insightful to eccentric and wrong. We analyse NOPCSA's studies in terms of their contemporary impact on the natural sciences and their relevance to modern research. Several interesting facets of his papers emerge: The mere existence of NOPCSA's volcanological hypotheses, including rifting and subduction, his extensions and corrections to neo-Lamarckian evolution, functional morphology of the origin of avian flight, and his advocacy of broad eclectic research programmes.

Zusammenfassung

Aus dem umfangreichen Werk von FRANZ Baron NOPCSA werden die Arbeiten und Bücher über fossile Reptilien, Invertebraten (*Kerunia*), Evolutionstheorie und theoretische Tektonik analysiert. NOPCSAs Leben und Werk wurde in kurzen Nachrufen (LAMBRECHT, 1933; EDINGER, 1934, 1955; F. E. SUESS, 1933; WOODWARD, 1934), in einer Biographie (KUBACSKA, 1945) und in Handbuchartikeln (LAMBRECHT et al., 1938; ZAPFE, 1978) beschrieben, aber noch nie wissenschaftsgeschichtlich untersucht. NOPCSA ist im Wesentlichen bis heute als Dinosaurierspezialist bekannt. Es zeigt sich jedoch, daß NOPCSA sich mit seinen Publikationen und Vorträgen entschieden gegen einseitiges Spezialistentum wandte. NOPCSA war viel mehr ein sehr vielseitiger Theoretiker, der seine eigentliche Leistung in der Synthese getrennter Arbeitsgebiete, im Übertragen von Konzepten auf neue Anwendungsgebiete und im Auffinden und Lösen von Anomalien und Paradoxien sah. Wir untersuchten NOPCSAs Ideen zu einzelnen Problemen, ihre Rezeption durch Zeitgenossen und ihr Nachwirken bis in die heutige Zeit. NOPCSAs kühne Konzeptionen haben in den meisten Fällen zu fruchtbaren Diskussionen angeregt, auch wenn sich einige seiner Lösungen sehr bald als unhaltbar erwiesen haben.

Als Reptilpaläontologe beschrieb und revidierte NOPCSA nicht nur zahlreiche Dinosaurier-Taxa, er führte auch zahlreiche neue Gesichtspunkte ein (Sexualdimorphismus, Biogeographie, Schädelkinetik) und führte andere erfolgreich fort (Biomechanik, Knochenhistologie). NOPCSA setzte sich vehement für das Modell der Vogel-Entstehung aus biped laufenden (nicht arborikolen) Reptilien ein.

Bei der Interpretation von *Kerunia* (einer Hydrozoe aus dem Eozän) entwickelte NOPCSA ein elegantes (wenn auch falsches) Modell einer Symbiose zwischen einem schalenlosen Cephalopoden und einer Hydrozoe.

In einer Zeit, wo der Neolamarckismus von den meisten Biologen und Paläontologen unkritisch akzeptiert wurde, erkannte NOPCSA die Schwierigkeiten dieser Evolutionstheorie. Er entwickelte eine Korrektur des Neolamarckismus, ohne in die dogmatische Einseitigkeit der Orthogenese-Theorie zu verfallen, mit der einzelne andere Autoren den Neolamarckismus zu überwinden versuchten. Er fand den Mechanismus, der die LA-

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MARCKschen Thesen (Gebrauch und Nichtgebrauch der Organe; Vererbung erworbener Eigenschaften) nicht in Frage stellte, aber gleichzeitig das Aussterben von Taxa verständlich machte, in der „Arrostie". Arrostie ist die lang anhaltende Störung des Hormonsystems, die zunächst zu (adaptiven) Veränderungen in Körpergröße und Körperbau, aber letzlich zum Aussterben führt. Nach NOPCSAs Tod überwogen zunächst die Einflüsse der Orthogenese-Theorien bis sich die Synthetische Theorie durchsetzte. NOPCSAs Korrektur des Neolamarckismus blieb daher weitgehend unbekannt.

Trotz seiner umfangreichen Erfahrungen in der Geologie Albaniens blieb NOPCSA ein Außenseiter in der Diskussion theoretischer tektonischer Probleme. Er demonstrierte die Fruchtbarkeit des Deckenmodelles und wandte die WEGENERsche Kontinentalverschiebungstheorie auf Probleme der Biogeographie an. In einer weitgehend unbekannt gebliebenen Arbeit (1927a) erklärte er Orogenesen als gigantische Überschiebungen von Sialplatten und zeigte, daß Magmatismus vom atlantischen, vom pazifischen und vom gemischten Typ an verschiedene Regionen und Entwicklungsumstände eines Orogens und an Spalten, die beim Auseinanderdriften von Kontinentalblökken entstehen, gebunden ist. NOPCSA hat damit wichtige Aspekte der Plattentektonik vorweg genommen.

NOPCSAs letzte Arbeit ist ein Schema vom Ablauf der Erdgeschichte, das auf der Vorstellung orogenetischer Zyklen und auf der Kontinentalverschiebungstheorie basierte.

1. Introduction

„Personalia: Died: Dr. FRANZ Baron NOPCSA in Vienna on the 25th of April at the age of 56. For a long time he directed the Hungarian Geological Survey and made merit for himself as an unusually manysided and spirited scholar, especially in the investigation of Albanian geology and the paleontology of reptiles." This anonymous obituary, published in 1933 in the Centralblatt für Mineralogie, Geologie und Paläontologie, summarizes all that is commonly known about FRANZ Baron NOPCSA VON FELSŐ-SZILVÁS, a familiar figure in vertebrate paleontology (Fig. 1). However, even allowing for a few obituaries and memorials, NOPCSA is very poorly known today. Indeed his work has never been studied from a theoretical point of view and it is our purpose to outline the highlights of his work as a progenitor to today's concept of paleobiology and continental drift.

Born 3 May, 1877, near Hatszeg, Hungary (now part of western Roumania), NOPCSA attended and received his Abitur from the Theresianum in Vienna and went on to the University of Vienna in 1898. NOPCSA's first contact with vertebrate paleontology was rather coincidental; in 1895 fossil reptile bones were discovered by his sister on the family estate near Szentpéterfalva and these NOPCSA showed to Prof. Dr. E. SUESS at the University of Vienna. SUESS apparently planned formal excavations but they were never undertaken. On his second visit with SUESS, NOPCSA was told to conduct a study of the Szentpéterfalva material by himself. This work culminated in NOPCSA's first paleontological contribution, on a new hadrosaurid dinosaur from the Siebenbürgen region of Hungary, at the Vienna Academy of Science on 21 June, 1899. Also in 1899, NOPCSA made his first journey to Albania, a country which fascinated him for the rest of his life.

While still at the Theresianum, NOPCSA met OTHENIO ABEL. ABEL, then a graduate assistant to E. SUESS, became well known along with NOPCSA as one of Europe's earliest paleobiologists (EHRENBERG, 1975; REIF, 1980). NOPCSA graduated from the University of Vienna in 1904 and in the same year met LOUIS DOLLO in Brussels. Influenced by DOLLO even before this meeting,

Fig. 1: FRANZ Baron NOPCSA (Drawing by F. MÁRTON, 1926 [from KUBACSKA, 1945]).

NOPCSA continued to acknowledge DOLLO's contribution to paleontology in numerous subsequent papers.

NOPCSA published a total of 158 papers (101 of them in paleontology) before his death in 1933. These works span such topics as paleobiology and taxonomy of lower tetrapods (particularly dinosaurs, but also including turtles, squamates and pterosaurs), bird flight, evolutionary theory, paleophysiology, paleohistology, archaeology, ethnology, geology and Albanian geography. NOPCSA's primary research areas were dinosaur paleobiology and systematics (42 papers), although he also discussed other archosaurs (5 papers on crocodilians, 4 on pterosaurs), lepidosaurs (11 papers), therapsids (4 papers), turtles (7 papers), ichthyosaurs (1 paper) and amphibians (1 paper).

NOPCSA seems to have had a good understandig of his international audience. He published primarily in German (114 papers) including the bulk of his tectonic work and in part reflecting his close personal ties with Vienna and its academy early in his career. However, important papers which strike an international pose (e. g. 1905e, 1907, 1923e, 1926b, 1928c, 1929a, 1934) were commonly written in English for both English-language and German-language journals (31 papers). He published 9 papers (primarily on geology but also on paleontology) in Hungarian, his native tongue, and additionally 5 papers in French on fossil material found in Normandy and Central France.

In 1920, NOPCSA was offered membership in the Geological Survey of Roumania which he declined. However, he became Director of the Royal Hungarian Geological Survey in 1925. This he resigned in 1929. He continued his paleontological and geological work until 1933, when he committed suicide on 25 April.

During his lifetime, NOPCSA kept a diary which was read by K. LAMBRECHT and A. T. KUBACSKA, two of his biographers. Presumably from his diary and other memorabilia, NOPCSA wrote an autobiography which was never published (KUBACSKA, 1945, p. 275). The only available material on NOPCSA are the few obituaries and memorials (LAMBRECHT, 1933; LAMBRECHT et al., 1938; EDINGER, 1934, 1955; F. E. SUESS, 1933; WOODWARD, 1934, ZAPFE, 1978) and KUBACSKA's biography (1945). It is unknown to us whether the NOPCSA estate still exists in the National Museum of Hungary in Budapest. Additionally, the VON HUENE archives in the Institut und Museum für Geologie und Paläontologie, Universität Tübingen, contains 45 postcards and letters from FRANZ BARON NOPCSA to FRIEDRICH VON HUENE.

Table 1: VON HUENE's and NOPCSA's Dinosaur Taxonomies.

VON HUENE (1914)	NOPCSA (1923)
Ramus Sauromorpha (= diapsids)	[Subclass Archosauria]
	Supraorder Dinosauria
Order Saurischia	Order Saurischia
Suborder Coelosauria	Suborder Pachypodosauria (= prosauropods)
Suborder Pachypodosauria (= carnosaurs, prosauropods, sauropods)	
	Suborder Coelosauria
	Suborder Megalosauria
	Suborder Sauropoda
Order Ornithischia	Order Orthropoda
Suborder Ornithopoda	Suborder Poposauria (= *Poposaurus*)
Suborder Thyreophora (= stegosaurs, ankylosaurs)	Suborder Ornithopoda
	Suborder Thyreophora (=ceratopsians, stegosaurs, ankylosaurs)
Suborder Ponderopoda (= ceratopsians)	

2. Dinosaur Systematics and Paleobiology

Probably NOPCSA's broadest and most accessible works for the present generation of reptilian paleontologists are his studies of the taxonomy and phylogenetic relationships among fossil reptiles. His best known studies, Die Familien der Reptilien (1923d), The Genera of Reptiles (1928c) and Osteologia reptilium recentium et fossilium (1931) helped establish taxonomic diversity among fossil reptiles during the early part of this century.

NOPCSA's tomes on reptile taxonomy were based in large part on more than 50 papers on the anatomy and taxonomy of widely diverse groups of fossil reptiles. These range from original descriptions of new taxa (1900, 1903a, 1923f, 1929c, 1930), revised accounts of old taxa (1902, 1903a, 1905a,b,c, 1911, 1912, 1923g), and studies of phylogenetic relationships among reptiles (1903b, 1910, 1925b, 1932c). The constant stream of NOPCSA's research on fossil reptiles parallels that of the other prominent reptilian paleontologist in Europe and NOPCSA's good friend and long-standig colleague, FRIEDRICH FREIHERR VON HUENE of Tübingen, Germany. NOPCSA was a frequent and favorite guest of the VON HUENE family (U. VON HUENE, pers. comm., 1983) and for 25 years they exchanged correspondence on respective research projects (KUBACSKA, 1945), reflecting a continued exchange of ideas in their studies of fossil reptiles.

Since both NOPCSA's and VON HUENE's main area of research was on dinosaurs, it is interesting to note that their work diverged dramatically on the question of dinosaur relationships and the concept of the Dinosauria as a natural group. VON HUENE, beginning in 1914, provided new and important support for SEELEY's (1887) separation of OWEN's (1842) Dinosauria into the Saurischia (including carnivorous and the gigantic sauropod dinosaurs) and the Ornithischia (remaining herbivorous groups). In doing so, VON HUENE always considered the Saurischia and Ornithischia to be distinct groups without close common ancestry. NOPCSA (1917b, 1922, 1923d), accepting the dichotomy implicit between saurischians and ornithischians (Orthopoda of NOPCSA), suggested that at the supraordinal level these two groups were more closely related to each other than to any archosaur group. NOPCSA's and VON HUENE's taxonomies of dinosaur relationships are given in Table 1. Since the 1920s, much work has been done on „within-group" taxonomy and phylogenetics of dinosaurs (much by VON HUENE, but also by COLBERT, GILMORE, LULL, PARKS and STERNBERG, to name a few). Yet the debate over phylogenetic relations of and between dinosaurs and their subdivisions, begun ultimately between OWEN and SEELEY, goes on unabated today (cf. BAKKER & GALTON, 1974; BAKKER, 1980; BONAPARTE, 1976; CHARIG, 1976, 1982). The issues of ancestor-descendant versus sister-group relationships and vertical versus horizontal classification schemes are still cloudy and it will take incisive and broad research on all archosaur groups before a clear solution to dinosaur taxonomy and phylogenetic is in sight.

At a time when descriptive studies of dinosaur remains had become commonplace, NOPCSA wrote a series of innovative papers which combined osteological description with discussion of soft anatomy in fossil archosaurs (e. g. 1900, 1902, 1903a). Most of his work pertained to cranial musculature and neuroanatomy in dinosaurs which, as is well known, lack modern relatives from which to extrapolate soft-tissue anatomy, physiology, or behavior. Influenced most strongly by DOLLO's (1883, 1884) studies of the cranial and skeletal reconstructions of Iguanodon, NOPCSA discussed the anatomy implicit not only in his dinosaur material from Siebenbürgen (1900, 1902, 1903a, 1929b), but also including ankylosaur material from North America (1928a). Although he never published many details of the reptilian postcrania, these ideas were certainly not foreign to him (letter of 3 October 1929 to VON HUENE discusses sauropod muscle reconstructions as a means to analyze body posture, limb movement and gait; KUBACSKA, 1945). NOPCSA's studies, along with those of his contemporaries LULL (1908), OSBORN (1912), BROWN (1914), RUSSELL (1935) and LULL & WRIGHT

(1942), represent an emerging interest in dinosaur biology that transcends the then common osteological descriptions of taxa. These were the works which tackled the problem of understanding animals long since extinct and so different from their extant relatives as to exclude most inferences about how these animals functioned and how they fitted into their ecological setting. It is on these initial studies that much of today's dinosaur paleobiology is built.

3. Biogeography of the Cretaceous Siebenbürgen Island

As alluded to in the introduction, NOPCSA's original work on the Siebenbürgen fauna of Roumania (Maestrichtian; JELETZKY, 1963) was the mainstay of his dinosaur work, producing important studies of the anatomy and taxonomy of 8 or so species of dinosaurs and other reptiles. Because of its location and the peculiar aspects of its fauna, the Siebenbürgen material also lent itself to discussion of the relationship between island faunas, body size, species richness and evolutionary atavism. Late in his career, NOPCSA (1923c, 1934) began synthesizing taxonomic, ecologic and biogeographic data to present a model of Siebenbürgen as an isolated Late Cretaceous island. NOPCSA then argued that the fauna consisted of isolated descendants of much earlier and more cosmopolitan terrestrial reptiles. Body size is lower among the Siebenbürgen animals relative to their ancestors als well as their closest contemporary relatives on the mainland and, NOPCSA pointed out, they are less diverse and retain the primitive nature of their ancestors. NOPCSA's work and its implication to other Late Cretaceous terrestrial communities in Europe (viz. LAPPARENT, 1947; PARIS &TAQUET, 1973; LAPPARENT & AGUIRE, 1956; SEELEY, 1881, 1883) have been largely ignored since the early part of this century (although see MOLNAR, 1980). These faunas and the Siebenbürgen fauna are in great need of reexamination. NOPCSA's broad paleoecologic and evolutionary outlook on his unusual Siebenbürgen fauna is both heterodox and interesting for its time, yet by today's view of island biogeography often incomplete or wrong-headed.

4. Dinosaur Jaw Mechanics

That analysis of vertebrate jaw mechanisms is important to trophic paleoecology and evolutionary character transformation is now ably expressed by the many papers on the subject (ALLIN, 1976; BARGHUSEN, 1968; BRAMBLE, 1978; DEMAR & BARGHUSEN, 1972; GREAVES, 1978). Although most deal with the evolution of the mammalian jaw, considerable work has been done on jaw systems in reptiles, the modern approach having its roots in the studies of STANNIUS (1856), VERSLUYS, LAKJER and LUTHER. However, the early work of NOPCSA, based on dinosaur material from Transsilvania, Hungary, influenced to a great degree the ideas of these and other authors, especially on intracranial mobilitv in recent and fossil reptiles.

NOPCSA's first paleontological paper (1900) considered the possibility of intracranial mobility in the hadrosaurid dinosaur *Telmatosaurus (= Limnosaurus) transsylvanicus*, now stored in the British Museum (Natural History). Based in part on comments by MARSH (1893) and by analogy with modern lacertilians, NOPCSA suggested that the quadrate bone was able to swing in a fore and aft direction (streptostyly; a term coined originally by STANNIUS, 1856). NOPCSA did not elaborate the details of jaw mechanics in hadrosaurids (1900), nor in other ornithopod dinosaurs (1902, 1903a), but rather discussed his ideas as asides in descriptive sections of his early and otherwise standard monographs. Nor did he follow up on his jaw mechanics work after 1903 or provide a clear understanding of the implications of his model of intracranial mobility in this group of dinosaurs. NOPCSA's suggestion that at least some kinds of dinosaurs had a movable quadrate might have been buried in the annals of descriptive paleontology had it not been for the detailed work on reptilian cranial morphology by J. VERSLUYS. In his monograph (1910, 1912) which came out of a 2-year visit to the U. S. A., VERSLUYS analyzed the broad question on intracranial mobility including streptostyly in reptiles and birds. In these papers VERSLUYS rejected NOPCSA's model of quadrate movement in hadrosaurs. However, in 1923, in a detailed study of the famous hadrosaurid „mummy" in the Naturmuseum Senckenberg, Frankfurt am Main, VERSLUYS reversed his earlier opinion. He outlined a new jaw mechanisms which incorporated NOPCSA's original views of fore-aft quadrate mobility and included an additional medial rotation of the mandibles about their long axes. In Europe, the interesting theme of intracranial mobility was carried on by VON KRIPP(1933c). However, he departed to a considerable degree from both NOPCSA's and VERSLUYS' models. VON KRIPP's work on jaw mechanisms in hadrosaurids stems from his then-current kinematic analyses of intracranial mobility of bird skulls (1933a, b) and seems to represent a side-issue for him. Yet his work was to break largely with the tradition of using joint morphology as the basis for erecting a mechanism; rather VON KRIPP used kinematic diagrams of 3-dimensional mechanisms modeled on joint morpholgy and joint position to graphically simulate the working of the jaws. Through this new approach VON KRIPP justified a new jaw mechanism for hadrosaurids. He rejected fore-aft quadrate mobility and medial rotation of the mandibles, instead outlining a jaw mechanism based on lateromedial movement of the quadrate and lateral rotation of the mandibles. Surprisingly, VON KRIPP's mechanism is based on the same Senckenberg hadrosaurid „mummy" which had been the foundation of VERSLUYS's mechanism. VON KRIPP's work however, represents a more rigorous attack on the problem of modeling jaw mechanism in extinct animals by graphically analyzing coordinated quadrare and mandibular movement in conjuction with observations of tooth wear.

NOPCSA's early work on hadrosaurid jaw mechanics had the effect of establishing a polarity between European and North American paleobiologists working on the same problem. The North American response (LAMBE, 1920; LULL & WRIGHT, 1942; OSTROM, 1961) rejected intracranial mobility in favor of rigid skull mechanisms. LAMBE rejected movement of the quadrate on the basis of joint morphology and structural constraints within the skull in his description of the hadrosaurid *Edmontosaurus regalis*. Rather, he suggested that hadrosaurid jaw mechanisms consisted of simple jaw closing and nearvertical shearing of the lower teeth past those in the upper jaws. LAMBE's mechanism was followed without comment in the first survey work on hadrosaurids by LULL & WRIGHT (1942).

OSTROM (1961) also rejected intracranial mobility in hadrosaurids based on structural constraints and instead indicated that jaw movement occurred slowly by means of fore-aft translation at the jaw joint. Like VON KRIPP, OSTROM used several aspects of tooth wear to support his hypothesis.

NOPCSA's model of hadrosaurid jaw mechanics as well as those of VERSLUYS, VON KRIPP and others, have recently been reanalyzed by WEISHAMPEL (1981, in press a, in press b) using 3-dimensional computer analyses. These previously mentioned mechanisms fail to model tooth wear in accordance with hadrosaurid real dentitions. Rather, hadrosaurid mechanisms consist of mobile upper jaws, (maxillae and several other facial bones) which can rotate laterally along a slightly inclined hinge joint. Only in this way was it possible for hadrosaurids to chew side-to-side while the jaws remained isognathous (i. e. producing bilateral occlusion), something NOPCSA failed to observe.

5. Sexual Dimorphism

For paleontologists who have worked on dinosaurs, NOPCSA is perhaps best known for his 1929 (a) work on supposed sexual dimorphism in these animals, undoubtedly because the paper is in English and because the geological raw data are so at odds with the anatomic basis for his theory. It is rarely discussed, however, that NOPCSA's interest in the impact of sexual dimorphism on reptilian taxonomy extends back to 1905(e) when he adduced evidence for the presence of sauropod os penis from an enigmatic bone which was previously interpreted as a clavicle (HATCHER, 1901). The identification of this bone in terms of its primary sexual characteristics was a novel anatomic approach but met with considerable resistance. HOLLANDS (1906), TORNIER (1909), and ABEL (1910) all rejected NOPCSA's contention, the last two authors calling the bone an episternal or first rib, respectively. NOPCSA again returned to the subject of the sauropod os penis in 1918, but merely reiterated his earlier arguments. No one has since advocated or refuted NOPCSA's hypothesis; indeed it is never discussed in present-day literature. Hence, it seems that NOPCSA's idea that an os penis was present in sauropods is a dead issue. Yet, what is of overriding importance is that he tried to understand how sexes among fossil reptiles might be identified in a biologically reasonable manner.

NOPCSA came back to the sauropod os penis in later work on sexual dimorphism and dinosaur taxonomy. Rather than arguing from the basis of supposed primary sexual characteristics, as in his 1905 paper, NOPCSA (1915, 1928a, 1929a) turned to identifying what he believed were secondary sexual characteristics. He argued that the fossil record of dinosaurs is dominated with examples of sympatric species pairs. From these pairs, he itemized the then obvious dimorphism. Skull shape, vertebral form and relative size of limb bones were ascribed to secondary sexual characteristics. The shape of the distal ischium was related to the attachment of penile musculature. By combining species of different genera into male and female pairs, he thought to establish a revised dinosaur taxonomy. In his short discussion (1929a), NOPCSA identified several small hadrosaurid genera as subadults of other taxa (cf. NOPCSA & HEIDSIECK, 1933; DODSON, 1975) and argued for such sophisticated social behaviour as display, social hierarchies and parental care among several groups of ornithopods (for a modern treatment, see HORNER & MAKELA, 1979; HORNER, 1982). NOPCSA's sexual dimorphism hypothesis however had several fatal flaws. Both STERNBERG (1935) and RUSSELL (1946) pointed out that NOPCSA's males and females rarely occur sympatrically over wide stratigraphic intervals and hence are of little taxonomic or paleobiologic value. That is not to say that the analysis of sexual dimorphism among fossil reptiles has had a waning history since NOPCSA's time. Indeed, the practice of identifying sexes and growth series among these animals has been fruitfully applied to several reptile groups in order to rectify taxonomic and paleoecologic problems. Immediately following NOPCSA's work, several studies used presumed secondary sexual characteristics to qualitatively sex fossil reptiles and establish growth series: BROILI & SCHRÖDER (1937) on *Dicynodon*; BROWN & SCHLAIKJER (1940) on *Protoceratops*, and VAUGHN (1966) on *Seymouria*. These isolated studies, the now classical synthesis on sexual selection and the fossil record by DAVITASHVILI (1961), and HOPSON's (1975) work on sexual selection and hadrosaurid dinosaurs round out the qualitative treatment of sexual dimorphism in fossil reptiles since NOPCSA's time. Access to highspeed computers have made quantitative studies of growth and sexual dimorphism in fossil reptiles almost commonplace. The most important of these (in one sense, descendant pieces of NOPCSA with a numerical bent) include DODSON (1975, 1976) on lambeosaurine hadrosaurids and *Protoceratops*, respectively, and GRINE & HAHN (1978), GRINE et al. (1978) and BRADU & GRINE (1979) on the therapsid *Diademodon*. It is likely, that sexual dimorphism, once introduced by NOPCSA to crudely explain the shapes of bones or skeletal configurations in dinosaurs, will appear in more studies of evolutionary ecology and taxonomy in fossil reptiles, among other organisms. Despite being absolutely wrong in his work on sexual dimorphism in these animals, NOPCSA's legacy is certain to be fulfilled.

6. Paleohistology

Starting in 1924, NOPCSA became interested in bone histology as a means to identify reptilian taxa on the basis of small scraps of bone. His published work, which began in 1925, was hardly more advanced than such special-interest studies as MANTELL (1850a, b), OWEN (1859) and BROILI (1922), in which whole bones or bone fragments were sectioned to document either internal morphology or identify the animal. Similarly, the comprehensive work of QUECKETT (1855) and SEITZ (1907) was intended for anatomic and taxonomic comparison, but over a wide variety of animals. The primary source for NOPCSA's slides was his own reptile material from the Siebenbürgen area, but in 1924 VON HUENE sent additional material from the Tübingen collections to NOPCSA to be thin-sectioned (letter of 1 August, 1924; KUBACSKA, 1945). NOPCSA also received bone specimens from the British Museum (Natural History), the Royal Ontario Museum and the American Museum of Natural History. By 1925, NOPCSA had amassed a collection of more than 500 histologic slides pertainig to 86 fossil reptile genera (letter to VON HUENE, 25 March 1925; KUBACSKA, 1945). As mentioned above, NOPCSA's first paleohistology paper (NOPCSA, 1925; not listed in RICQLÈS, 1980) intended to provide histologic discrimination of fossil reptiles from Nigeria, based on fragments of femora, humeri and unidentifiable bone. However, in later studies he recognized that histologic structure may change from site to site within the skeleton due to a variety of factors, among them stress and growth rates. NOPCSA ultimately chose to section ribs of fossil reptiles, arguing that their mechanical loading would be similar among all groups regardless of size or growth rates (letter to VON HUENE, 6 June 1929; KUBACSKA, 1945). In one of his last two histologic papers done in collaboration with E. HEIDSIECK, NOPCSA used rib histology to solve the problem of differentiating juveniles from small adults, recognizing conspecific juveniles and adults which had hitherto been assigned to different species (NOPCSA & HEIDSIECK, 1933).

Apparently NOPCSA hoped to conduct a thorough histologic study of all fossil reptiles (see numerous comments in KUBACSKA, 1945), but its future was cut short by NOPCSA's death in 1933. The whereabouts of his histologic thin sections are unknown to us. Such work was not to resume again until the 1950s and 60s with the survey work of ENLOW & BROWN (1956, 1957, 1958). Current work, often as a tool to understanding paleophysiology from bone microstructure, can be found in studies of RICQLÈS (e. g. 1980).

7. Origin of Flight

The discovery of *Archaeopteryx* brought to the paleontological forefront the concept of evolutionary intermediates, in this case at the class level between Reptilia and Aves. This unique status has generated two partly-dependent evolutionary questions. First, what are the phylogenetic relationships of *Archaeopteryx*? Second, what can *Archaeopteryx* reveal about the evolutionary history of avian flight? OSTROM, (1976), TARSITANO & HECHT (1980), HECHT & TARSITANO (1983) and THULBORN & HAMLEY (1982) review in some detail the first question, for which it has been suggested that bird origins can be found among such different groups as pseudosuchian thecodontians, crocodilians, ornithopod dinosaurs and theropod dinosaurs. NOPCSA's work on bird origins (1907, 1923e, 1927c, 1929b) does not deal explicitly with phylogenetics; he denoted avian ancestry wihtin a rather vague dinosaur-like group of animals. It is not clear whether he considererd this group as belonging among pseudosuchians (thecodontians) or among dinosaurs. His 1929 comments about a relationship with „*Proterosaurus*" [= ?*Proterosuchus*] are vague and, we consider, misleading. What is important in NOPCSA's discussion of avian origins is his consideration of the evolution of bird flight.

In 1907, the prevailing theory of the origin of bird flight maintained that it arose among tree-dwelling reptiles (MARSH, 1880; HURST, 1895; PYCRAFT, 1894a, b, 1896). The process of branch-hopping led to gliding structures and finally to wings involved in powered flight. In all cases, thecodontians were envisioned as the group that spawned arboreally-derived flight.

In direct opposition to the arboreal theory of avian flight and evolution from thecodontians, NOPCSA elaborated the concept of a cursorial origin, whose progenitors as mentioned above were small, lightweight, dinosaur-like animals. Although not the first to argue cursorial origin or dinosaur/dinosaur-like ancestry for birds (viz. WILLISTON, 1879) it is clear that NOPCSA was the most ardent and articulate supporter of, as he termed it, the "running pro-avis" concept. In contrast to WILLISTON, NOPCSA substantiated his theory through several new lines of evidence. He argued that in vertebrates there exists a fundamental dichotomy in flight mechanism that can arise from either a quadrupedal or a bipedal ancestor. Quadrupedal ancestors evolve a flight apparatus consisting of both fore- and hindlimbs plus extensive patagium. In this way, the patagium effectively supports the body at its center of gravity and flight consists first in gliding and secondarilay in powered flight. Bipedal locomotion allows tow-fold limb specialization:

1. the development of hindlimb construction for cursorial locomotion and
2. independent forelimb specialization, including the development of a small patagium and thus foreshadowing the avian wing.

Since only the forelimb in birds, including *Archaeopteryx*, is involved in the flight apparatus, NOPCSA argued that birds must have evolved from a bipedal cursorial ancestor. As a likely consequence, powered flight arose first, while gliding developed as a secondary achievement. In support of his theory, NOPCSA referred to *Archaeopteryx* and modern birds, citing highly modified cursiorial features of the hindlimb (e. g. reduction of pedal digits to a tridactyl condition, digitigrade stance, elongated tibia and fibula relative to the femur) in comparison to the less modified forelimb construction and the long neck. Before the forelimb evolved into a wing, the hindlimb developed as a cursorial functional complex, and hence, birds must have been bipedal cursors before they could fly.

In answer to the commonly held view that the avian furcula represent fused paired clavicles in reptiles, he advanced the idea (1923e, 1929b) that this homology does not exist. Rather the furcula sprang de novo as an ossificatioan of a tendon extending from the scapulocoracoid to the sternum and acting as an important support between the sternum and shoulder girdle. That such a tendon would have been loaded in tension and the furcula in compression seems not to have occurred to him and currently the furcula is believed to represent co-ossified clavicles of dermal origin (VAN TYNE & BERGER, 1959).

NOPCSA touched briefly on the selective advantage of feathers in 1929. He agreed with earlier authors that feathers had not initially evolved as a funtional response to flight. Rather, he explored the possibility that their initial selective advantage was insulatory. Because he believed that the dinosaur (or dinosaur-like) bird dichotomy may have taken place in the Permian, glacial conditions then-existing would have placed a premium on insulatory structures – such as feathers – in conjunction with small size and elevated metabolic rates.

NOPCSA's running pro-avis hypothesis was criticized in Europe and North America (HAY, 1910; ABEL, 1912; BEEBE, 1915; STEINER, 1917) but later was ignored after the publication of HEILMANN's treatise on the origin of birds (1927). This work championed both the arboreal theory and thecodontian ancestry.

It is not well understood how much influence NOPCSA's works have had on discussions of the origin of avian flight, so long has HEILMANN's study been in the vanguard. Later writings only elaborate the ancestry of *Archaeopteryx* (DE BEER, 1954, 1964) or adaptive aspects of the arboreal theory (BOCK, 1965). However, if he is correct, OSTROM's (1973, 1974, 1976) theory of a cursorial, predaceous origin for bird flight, vindicates NOPCSA's opinion of the relationship between bipedality and flight. They differ with regard to the adaptive basis for the development of feathered wings. For NOPCSA, the flapping of proto-wings increased running speed; for OSTROM, they were used as insect nets. However, phylogenetic analyses of *Archaeopteryx* by TARSITANO & HECHT (1980; see also HECHT & TARSITASNO, 1983) cast doubt on OSTROM's conclusions about the relationship of *Archaeopteryx* and they further suggest that the origin of avian flight requires an intermediate arboreal stage.

A final twist to the avian flight story comes from a very recent biomechanical study of the physics of ground-originating flight (CAPLE, et al., 1983). They advocate, à la NOPCSA, a cursorial proavis but on sophisticated mechanistic grounds. This work suggests, if nothing else, that it is insufficient to use simple scenarios and functional morphology to explain the origin of flight from either the ground-up or tree-down.

8. Kerunia

One of the most charming papers by NOPCSA is that on *Kerunia* (NOPCSA, 1905d). *Kerunia cornuta* (Eocene, Fayum District, Egypt) is now known as a symbiosis between a pagurid hermit crab, which inhabits a snail-shell, and a hydractinian coelenterate. The hydractinian settles on the snail-shell and with its growing skeleton increases the "living chamber" of the pagurid (DACQUÉ, 1921, p. 471). *Kerunia* was discovered by the Swiss paleontologist K. MAYER-EYMAR (1900, 1901). MAYER-EYMAR regarded it as a cephalopod. OPPENHEIM (1902) discovered its true hydractinian nature on the basis of surface structures but was not interested in the fact that (as he assumed) *Kerunia* originally overgrew a mollusc shell which was later dissolved. Rather he was interested in taxonomic problems (should the species receive the generic name *Kerunia* or *Hydractinia*?) and in its regional and stratigraphic distribution.

NOPCSA found virtues in both these views of MAYER-EYMAR and of OPPENHEIM. He had collected *Kerunia* in Egypt (during a trip with his mother and his sister in 1904). He showed the specimens to R. BULLEN NEWTON, a specialist on Eocene cephalopods at the British Museum, who pointed out the great resemblance between *Kerunia* and the Eocene cephalopod *Belosepia*. With a cross-section of a complete specimen (Figs. 1 and 2 in NOPCSA, 1905d), NOPCSA demonstrated the similarity in the growth pattern between *Belosepia* and *Kerunia*. Because of the high regularity of the growth-pattern of *Kerunia*, NOPCSA clearly excluded the model of a hydractinian overgrowing a gastropod. Thin sections and surface structures clearly pointed out to NOPCSA that *Kerunia* is a hydractinian. NOPCSA found only one way out of this paradox and (despite the fact that he is completely wrong) it is a fascinating model which he developed: *Kerunia* is both a cephalopod and a hydractinian! It is a symbiosis of a *Belosepia*-like cephalopod and a hydractinian in which the hydractinian takes over completely the task of skeleton-building for the cephalopod. After the death of the cephalopod the hydractinian continues mineralizing and forms the typical irregular shape in which no specimen is exactly alike another. NOPCSA clearly pointed out that this model could be tested with the recent hydractinian-pagurid hermit crab symbiosis.

Several authors after NOPCSA confirmed that *Kerunia* was a hydractinian colony and H. DOUVILLÉ (1907) even found the snail shell around which the hydractinian had grown as predicted by OPPENHEIM. The problem was finally settled by EBERHARD FRAAS (1911) who published a specimen from a Recent *Hydractinia calcarea* which had overgrown a serpulid worm and which had the typical *Kerunia*-shape.

9. Evolution

It is unknown whether NOPCSA had a more than average familiarity with evolutionary theory, i. e. with the classical publications on Darwinism and on Lamarckism and with current discussions. However, there is hardly any doubt that NOPCSA knew the papers by JAEKEL (1894, 1902, 1913), HENNIG (1928, 1932) and a few other authors. In the 1920s when NOPCSA published his important papers, neo-Lamarckism had lost its monolithic importance and was gradually being replaced by the theory of orthogenesis. Standpoints which combined both views (i. e. neo-Lamarckism and orthogenesis) were regarded as quite acceptable by some authors. In neo-Lamarckism, evolutionary change is brought about by the need of the organism; in other words evolution is completely opportunistic and adaptive. In orthogenesis, evolutionary change is brought about by an internal program in the organism; in other words it is not opportunistic, but preprogrammed and not necessarily adaptive (REIF, in press). Compromises between both points of view seem to be feasible.

The reason for the various attempts between 1910 and 1930 to liberate paleontology from a dogmatic neo-Lamarckism is apparent. Evolution could not be interpreted as completely opportunistic, otherwise one would not observe extinction, long-term linear trends, and harmful characters (the famous sabre-tooth tiger comes to mind).

Two solutions to this paradox are important in German literature: ABEL's theory of 1928 and 1929 which laid the ground for orthogenesis and NOPCSA's theory which corrected neo-Lamarckism without accepting orthogenesis and which is hence a unique theory.

To solve the paradox (of opportunism and adaptation on the one hand and extinction, long-term trends and seemingly harmful characters on the other), ABEL suggested an all-encompassing theme, the principle of inertia, which underlies all evolution. This principle combines

1. EIMER's law of orthogenesis,
2. COPE's law of the unspecialized ancestor,
3. DOLLO's law of irreversibility and
4. ROSA's law of the increasing reduction of variability (REIF, in press).

From the mere enumeration of the laws which were combined, it is quite obvious that ABEL's principle could explain everything, adaptation as well as extinction, opportunism in evolution as well as longterm trends. The principle simply states that the evolutionary process has such a high inertia (in the strictest physical sense) that it can easily run beyond the adaptive realm into the area of hypertrophied organs and extinction.

NOPCSA's solution was quite different. In one of his first papers (1923a, see also 1926a) of the series, NOPCSA delt with DOLLO's law of irreversibility (the term had been coined by ABEL). He showed under which conditions evolution is irreversible (e. g. when a character is so strongly fixed that it cannot be altered) and additionally gave several cases of reversible evolution in fossil reptiles: if an organism faces an evolutionary dead-lock, it can only be saved from extinction by a reversal to an embryonic stage. The life history of an individual, seen as a distorted recapitulation of the history of its whole phylum, explains why a limited reversal of evolution can occur.

As early as 1917, NOPCSA approached his major theme, the relation between body size and the size of the pituitary fossa in dinosaurs, several years before the growth hormone was identified in the pituitary gland. With incrasing size of the pituitary fossa during evolution, the bones of the extremities become more masive. In an extensive review of literature on endocrinologic diseases, NOPCSA came to the conclusion that there is a relationship between these phenomena and acromegaly. This is a hyperfunction of the pituitary gland, which is connected with an increase in size of the pituitary fossa and which leads to gigantism and to extreme ossification in humans. Acromegaly was known to be sometimens hereditary and that it leads to a decrease in fertility and vitality. NOPCSA was very satisfied by this because this suggested an answer to why dinosaurs died out. He did not elaborate on the question of how dinosaurs might have acquired acromegaly nor how it became hereditary (NOPCSA apparently fully believed in LAMARCK's principle of the inheritance of acquired characters).

In 1923 (NOPCSA, 1923b), he discussed osteological phenomena in marine tetrapods which he explained by reference to the human diseases pachyostosis and osteosclerosis. "Pachyostosis" and "osteosclerosis" (in NOPCSA's interpretation) occur in marine tetrapods which have only recently invaded aquatic habitats. It is a physiological disturbance which is caused by the new milieu and which is often adaptive by influencing the buoyancy of the animals. In fully adapted marine tetrapods, "pachyostosis" and "osteosclerosis" are secondarily lost. The process of acquiring "pachyostosis" and "osteosclerosis" in aquatic tetrapods is usually harmless, because the results are spread over many generations. NOPCSA suggested the term "Arrostie" for these and the phenomena of gigantism in dinosaurs. The term indicates that important evolutionary changes were brought about by disease-like processes over many generations.

A summary of his views on evolution is given in NOPCSA (1926b): "In a certain sense the factors of heredity and evolution can only be studied on groups of animals with a history going back to far remote geological times. They must also have recent representatives, so that their biology can be known at least to some extent. They must show a good amount of variation and live in different media." There is no doubt that the higher vertebrates fulfill these requirements and that this is the justification for NOPCSA's paper. It is very characteristic for the time when NOPCSA wrote these lines that paleontologists had no inkling of how important laboratory genetics and population genetics were (or would later become) for the theory of evolution. They did not regard it as arrogant, let along anactualistic, to claim that the fossil record provided the relevant causal factors for the process of evolution.

NOPCSA delt with a variety of different problems:

1. Parallel evolution, which is caused by similar environmental stimuli on similarly structured tissues in closely related groups. These stimuli lead to newly acquired heritable characters.
2. Mechanically-induced convergence (e. g. torpedo shape in aquatic vertebrates) is caused by natural selection on newly acquired characters which are transmitted to the offspring.
3. Arrostic changes: pachyostosis is caused by a deficiency of air-supply in aquatic animals. The changes during the evolution of dinosaurs (size, tooth shape, pattern of bone calcification) can be explained by a disturbance of the hormone system. The disturbance, and this is NOPCSA's new idea, is caused by a change in food and in vitamin supply, leading to hereditary changes in physiology.
4. Cases of inheritance or traumatic irritations. Tumors, skin diseases (like keratosis) and traumatic lesions can, if massively accumulated, be regarded as primordial stages of horns, antlers and snout thickenings in mystriosuchid phytosaurs. By a change in function the primordial stages can be developed as fully functional structures. As growth and healing phenomena are accompanied by an activity of hormones, there is again no doubt that the above-mentioned disturbances become heritable by simply postulating that hormones "effect [affect] the constitution of the germplasm" (p. 646).
5. Inheritance of acquired characters can never be tested in experiments with living organisms. All experiments even over many generations seem like "child's play" (p. 648) from a paleontological point of view. "Even so much as one hundred generations means nothing in the eyes of a paleontologist" (p. 648). There is no doubt that NOPCSA is right here! There is no inductive experimental way through however many generations to disprove the inheritance of acquired characters. It is only by our understanding of the functional interrelationships between DNA, the different RNAs and various enzymes that we can deductively falsify the model of inheritance of acquired characters.

NOPCSA supported his case by citing numerous publications by zoologists on successful experiments and on the theoretical plausibility of the inheritance of acquired characters. He assumed that the degree of fixation of a character determines whether it can be altered by external stimuli. These alterations are "phenotypical" because they occur via the phenotype. Changes are inadaptive and lead to rapidly diverging lines (e. g. Latipinnatidae and Longipinnatidae in ichthyosaurs). "After this primary change, both groups evolve but slowly and exclusively on purely adaptive and mechanically-necessitated lines" (p. 652). This is neo-Lamarckism at its best! How can one expect that random mutations can lead to anything but inadaptive evolution? Evolution is adaptive and hence we have to point out the appropriate mechanisms (among them, the evolutionary potential of what we would today call "heterochrony").

In the last chapter the "axiom of irreversibility" is replaced by the "much less rigid rule: the marks of evolution are generally ineradicable." Here NOPCSA continues to fight the dogmatism of ABEL's "Law of DOLLO" and again he is right; only with an understanding (which we are approaching only today) of the function of the genome and epigenetic apparatus can one meaningfully discuss the question if irreversibility.

A short version of the 1926(b) paper was published in German in Natur und Museum (1927b). Interestingly enough this excerpt is accompanied by a neo-Lamarckian chapter from "Back to Methusala" by BERNHARD SHAW (an arrangement that was made by the editor of the journal).

We know from his biographers (EDINGER, 1933; LAMBRECHT, 1933; KUBACSKA, 1945) that NOPCSA was seriously ill in 1928 when, on his invitation, the annual meeting of the Paläontologische Gesellschaft took place in Budapest (1928b). NOPCSA read his welcoming address from a wheelchair. It is important to know that NOPCSA believed that he would never be able to work again (he was, however, wrong on this assumption) in order to appreciate that this address has to be read as his intellectual legacy. In the first paragraph NOPCSA emphasized both aspects of paleontology, "geo-paleontology" and "paleo-zoology" (he did not use ABEL's term paleobiology) only to demonstrate that both directions are important. Natural Science is one unit and it is only our weakness that we separate individual disciplines. "Der Nachteil der Zersplitterung der einheitlichen Naturwissenschaft liegt darin, daß brach liegende Grenzbegiete entstehen." The whole paper that follows is an entire argument against specialists who fight for the separation of disciplines and who never begin to touch the "Grenzgebiete", in other words those who avoid interdisciplinary work.

NOPCSA then gave a short survey of the history of paleontology and its different approaches. He extensively pointed out the virtues of ABEL's book on paleobiology (1911) and its neo-Lamarckian approach, only to conclude that not all observable evolutionary changes are explained by ABEL's neo-Lamarckian model (see also REIF, in press). Rather NOPCSA believed that ABEL neglected that an organism and "hence every skeleton" is not only a mechanically integrated but also physiologically integrated unit (p. 8). He then summarized his results on the inheritance of disturbances of the hormone system and of the effects of oxygen supply. His main interest was no longer in the pituitary gland but in the thyroid gland, a discussion of which he was never able to complete due to his bad health. He concluded that the mechanical adaptation of an organism during evolution is only possible to the degree that is allowed by its physiology; in other words, evolution is by no means as opportunistic as was claimed by orthodox neo-Lamarckians! Physiology plays such a dominating role that paralell evolution is quite common. A single species (he gives as an example *Mastodon*) can originate from its ancestral species in different areas (of Europe) at the same time because the same environmental stimulus hits the same physiological system in many animals at the same time. Arrostic processes can be strong, which makes taxonomy difficult (p. 15; it is not clear whether NOPCSA thinks of saltational processes here). However, if the arrostic processes are weak, mechanical adaptation leads to "schöne und systematisch leicht überschaubare Entwicklungsreihen" (p. 15). NOPCSA could not possibly have predicted the near end of the neo-Lamarckian era when he exclaimed: "Meine Herren! Mit schwacher Hand habe ich heute versucht, einen schweren Vorhang zu ziehen, um Ihnen ein neues Morgenrot zu zeigen. Ziehen Sie, namentlich die Jüngeren von Ihnen, an diesem Vorhange nur kräftig weiter; Sie werden bemerken, das Morgenrot wird immer röter und Sie werden einen Sonnenaufgang erleben."

This is NOPCSA's version of neo-Lamarckism which fascinates by its interdisciplinary outlook. NOPCSA was familiar not only with vertebrate anatomy, ecology, phylogeny and biomechanics, but also with the large literature of human pathology and endocrinology. ABEL, who developed his principle of inertia later, did not fully accept NOPCSA's theory. ABEL in his book of 1929 only mentioned two less important descriptive papers by NOPCSA, but he did not quote from the more important theoretical papers (NOPCSA, 1917a, 1923a, b, 1926a, b. 1927a, 1928b). Instead ABEL developed a view of evolution which was much more schematic (not to say dogmatic) and which led directly to orthogenesis (REIF, in press). It is fascinating to see how NOPCSA used examples of teratology, pathology and endocrinology to discover how evolutionary novelties are brought about, always assuming that acquired characters are, under certain circumstances, heritable. If disturbances to normal physiology are slow, they can, at least normally, be harmless and will be effective causes of evolutionary change. In the long run, however, as in the case of dinosaurs, they can be one factor for the extinction of a taxon. It is quite obvious that NOPCSA provided satisfactory answers to all problems faced by dogmatic neo-Lamarckism and that he avoided such dogmatism himself. The only problem is that he could not see in the maturing Mendelian genetics and in the tacitly developing population genetics the major lever arm which would remove neo-Lamarckism from its eminent position within 10 years after his own death.

10. Theoretical Tectonics

NOPCSA's contributions to geology will be mentioned only partly here. It is well known that he wrote more than 25 articles including a 700 page monograph on the regional geology and stratigraphy of Albania. This will not be discussed here. It suffices to mention that NOPCSA, a former student of E. SUESS, was well trained in field geology and well informed about the tectonic and geotectonic hypotheses of his time. To be expected, he was progressive rather than conservative in application of the nappe model to the reconstruction of the Dinarids. In a letter to A. WEGENER of Aug. 23, 1928, he called himself a supporter of WEGENER's theory from the beginning (KUBACSKA, 1945, p. 245).

The first paper which is of interest for us is the one page note in which NOPCSA pointed out that he had demonstrated overthrusts in northern Albania in several papers since 1906 (NOPCSA, 1921). NOPCSA complained that L. KOBER, a well known alpine geologist, had claimed in reviews of two NOPCSA papers and of a book by KOSSMAT, that he, KOBER, had discovered the nappestructure of the Dinarids in 1914 and that NOPCSA had always negated ist. NOPCSA's defense is clear but aggressive and it shows that he feared for his acceptance by the establishment of structural geologists. It seems as though he had every reason for this fear, because the revolutionary ideas which he later published were systematically neglected. Most if not all of his papers on paleontology and geology were "reviewed" in Geologisches Zentralblatt. This, however, means nothing because the "reviews" were simply short versions of the abstracts, or, at best, descriptions of the content of the papers. We have been unable to find any of NOPCSA's papers on theoretical geology quoted in summarizing books, textbooks, and those papers by wellknown structural geologists which we have checked. There is no doubt, however, that with respect to the re-

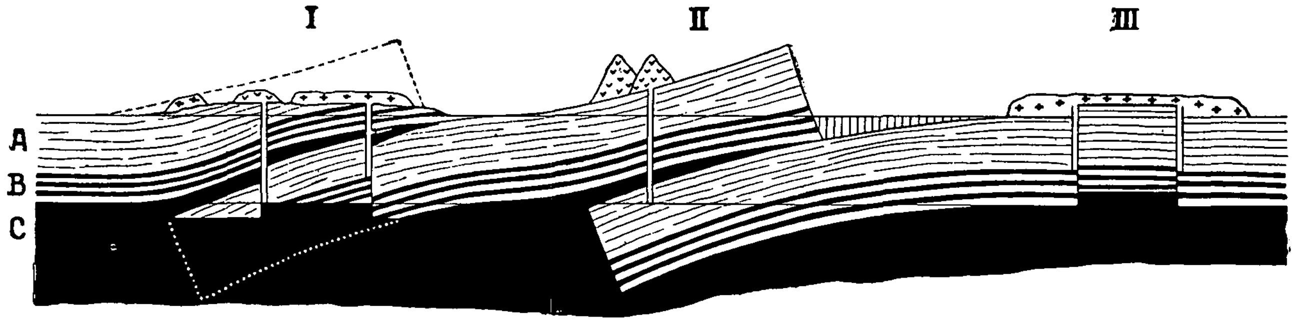

Fig. 1. [v v v] sauere Eruptiva. [+++] basische Eruptiva.

Figurenerklärung: *A* Obere Sialregion, *B* Untere Sialregion, *C* Simaregion. I. Alte abgetragene Gebirge mit späterem Schollenbau und gemischten späteren Eruptionen. II. Junge Faltengebirge mit inneren Vulkankranz (links), überschobener Stirne (Mitte) und vortiefe (rechts). III. Alte Tafelländer mit Deckenergüssen.

Fig. 2: NOPCSA's model of magmatic processes. A = upper sialic region; B = lower sialic region; C = simatic region; I = eroded mountain regions with postorogenetic structural overprint and mixed postorogenetic volcanic eruptions; II = young fold-mountains with an inner volcanic garland (left), an overthrusted front (center) and an outer trench (right); III = old continental plates with lava plateaus; vv = acidic eruptives; ++ = alkaline eruptives (from NOPCSA, 1927 a).

gional geology of Albania, NOPCSA held a virtual monopoly for several years which was accepted by most of his colleagues.

In a letter of Jan. 2, 1925 to F. VON HUENE, NOPCSA exclaimed: "Hurrah! Hurrah! Hurrah! that you have Karroo (South Africa) reptiles from Brazil. They must be the same or nearly the same forms as in Africa. Unfortunately I sent my manuscript on WEGENER's continental drift to England away already". We were unable to discover which paper NOPCSA meant and whether it was eventually published.

NOPCSA's first completely theoretical paper on tectonics (1927a) takes continental drift for granted and does not even mention WEGENER. By quoting only a few literature sources, NOPCSA demonstrated that the main structures of orogenies are gigantic overthrusts of sialic blocks. This model helped him, again by quoting only a few references, to explain the mechanisms of three types of magmatism, each of which is restricted to certain areas of a mountain region.The first type of magmatism which occurs on the inner, concave rim of mountain regions is acidic and consists of trachyte, andesite, dacite and rhyolite. This type is found in the circum-Pacific and the Eurasian meridional mountain regions: this is the Pacific-type of magmatism in SUESS' sense and NOPCSA explained it by a melting of the subducted sialic plate. The second type of magmatism is basaltic, occurring in the Pacific, in the Atlantic (Atlantic-type of magmatism sensu SUESS) and on consolidated sialic blocks (Syria, India, Australia, Antarctica, Canada, Brazil). The magmas are derived from melting simatic crust. The third type is a mixed type consisting of peridotites, serpentinites, diabases and gabbros which occur in the center of eroded mountain regions. Serpentinites and peridotites characteristically can be found in big overthrust zones. Peridotites, which chemically are simatic (high Mg content), were squeezed into the overthrust zone from below during orogenesis. With details from his hypothesis, NOPCSA explained why acidic magmatism is often ended by alkaline eruptions and alkaline magmatism often by acidic eruptions; a phenomenon which he called "inversion".

NOPCSA supported his model of the different origins of magmas by a careful discussion of available geochemical data. His diagram (1927a; see our fig. 2) is certainly the most spectacular part of his paper because it clearly shows subduction zones and their associated magmatism. In many details his model agrees with the modern view of magma origin. For all intents and purposes, NOPCSA's approach and his diagram are highly original. He must have developed it himself, since it appears that he cannot have "borrowed" it from other sources. Despite his originality, NOPCSA' model does not extend beyond the firm basis of WEGENER's Kontinentalverschiebungstheorie, namely the idea that sialic plates "swim" on the simatic crust. This is certainly a very important difference to the modern plate tectonics concept.

Geotectonic models were widely discussed in the 1920s. A critical summary is give by NÖLKE (1924) who concluded that among all the various models only the Theory of the Earth's Contraction (which had been strongly supported by E. SUESS) could be seriously held. The geophysicist KIRSCH (1928; 1938) summarised all data on radioactivity as an energy source for magmatism, convection in the Earth's mantle, and continental drift. However, even in his second book KIRSCH did not quote NOPCSA nor did he develop any model of subduction. The British geologist ARTHUR HOLMES is usually praised for having first developed (in 1929) a model of convection in the Earth's mantle which powered the drifting of crustal plates (HALLAM, 1973, p. 26; SCHWARZBACH, 1980, p. 98). However, it is only indicated by HALLAM (1973) but clearly shown by KIRSCH (1928, p. 76ff; KIRSCH seems to be completely forgotten today) that the foundation to this theory was laid much earlier. The roots can be found in HOLMES' own papers dating back at least to 1925 and JOLY's papers which date back much further (GREENE, 1982). The idea is summarised by F. E. SUESS in 1912. However this may be, it seems to be true that HOLMES (1929) developed an interesting and important model of convection. Orogeny in HOLMES' model is not a process of collision and subduction, but simply a process of jolting of areas where the convection current has a downward direction. Overthrusting and subduction of crustal plates are not included in HOLMES' model.

Only recently AMPFERER's Unterströmungstheorie has been "rediscovered" as one of the predecessors of WEGENER's continental drift hypothesis (K. SCHMIDT, 1976; for dates on AMPFERER, see SCHWARZBACH, 1980). As early as 1906, AMPFERER argued strongly against the Theory of the Earth's Contraction and instead suggested that the mechanics of the Earths's crust can be explained by subcrustal magma flow. In 1911, AMPFERER & HAMMER suggested a sucking-in of crustal parts "erdeinwärts" (= into the mantle?) which leads to a dense folding, overthrusting, and nappe formation of crustal parts.

AMPFERER (1925) very critically discussed WEGENER's theory. He did not accept that the sialic plates drift on the simatic layer, which would involve the acceptance of shear zones on the ocean floor. Rather the plane of mass transport must lie much deeper than assumed by WEGENER. AMPFERER also pointed out that the plates cannot be moved by outer forces but rather by inner ones. If America drifts westward, as AMPFERER accepted, oceanic crust must sink into the depths, only to reappear as oceanic crust in the Atlantic. This process of mass transport is at the same time the motor for plate movement. (AMPFERER did not point out that the energy source is radioactivity!). This means that convection processes transport the American continent, at the same time sucking in oceanic crust in the Pacific (which explains the deep sea trenches!) and reintegrating it by local eruptions in the Atlantic. AMPFERER did not provide any model of overthurst of sialic on simatic crust or of sialic on sialic crust. He strongly argued against the assumption that the Andes can be explained by a jolting of simatic crust or a sweeping together of the clastic detritus from the gradually eroded continental block. He left it completely open as to how the Andes formed and did not touch the problem of andesitic volcanism.

In German-speaking countries a connection between radioactivity and geological processes was first summarized by F. E. SUESS (1912). In a paper which was also only recently "rediscovered" by K. SCHMIDT (1976) and which was not quoted by NOPCSA, the geologist R. SCHWINNER (1920), Graz, Austria, developed a theory of thermal convection which strongly supports AMPFERER's models and which explains magmatism and tectonic processes. SCHWINNER accepted radioactivity as the energy source for all tectonic phenomena and introduced the term "tectonosphere". The tectonosphere includes all outer layers of the Earth down to the level where there is a hydrostatic gravitational equilibrium. According to SCHWINNER the tectonosphere is 120 km thick. SCHWINNER applied models from meteorology (cyclones and anticyclones) to discuss the processes in the tectonosphere and to explain orogenies and volcanism. He is most likely the first author to give schematical diagrams of thermal convection of the earth and his model of orogeny is similar to that of HOLMES (1929). Volcanism is exclusively explained by a "Zerrungstektonik" (extensional tectonics) of the crust. In other words, both specific features of NOPCSA's (1927) model, overthrusting of sialic plates during orogenies and regional differentiation of the different types of magmatism, are lacking.

It is not surprising that the revolutionary publications of WEGENER (1912, 1915) and of SCHWINNER (1920) were not mentioned by HANS STILLE in his "Grundfragen der vergleichenden Tektonik" (1924). AMPFERER is quoted only from his papers which describe structural data, but not from his theoretical papers. STILLE himself favored the Contraction Theory and was strongly fixistic; in other words, he rejected all plate movements, subductions, Unterströmungen, etc. STILLE's personal authority and especially his Grundfragen strongly influenced German geology well into the 1960s and 1970s (REIF, in press).

The only tectonic synthesis which NOPCSA (1927) quoted, but which we could not find referred to by other authors, is that of SANDBERG (1924). SANDBERG seems to have been an outsider in tectonics. He quoted only a few papers by himself which were published in German, French and English. He wrote his two-volume book in English which was translated into German by someone else. SANDBERG developed a fixistic theory, rejecting all plate movement and also the Contraction Theory. All tectonic processes ultimately are caused by vertical isostatic movements. The causes of the disturbance of isostasy are differential heat flow, erosion, sedimentation, melting, and compaction. NOPCSA did not state whether he agreed with SANDBERG or not; obviously he did not. NOPCSA only quoted some volcanological and sedimentological data from SANDBERG.

One should comment on K. SCHMIDT's (1976) "rediscoveries" of AMPFERER and SCHWINNER that these authors are not found in the English geological literature nor in the English literature on the history of continental drift and plate tectonics. However, in German literature these authors and their theoretical contributions have never been forgotten. A survey of the literature shows that both authors can be found in pre-war textbooks (CLOOS, 1936; BRINKMANN, 1940; probably also in earlier editions of this book) and in text-books of West Germany (BRINKMANN, 1976; ZEIL, 1975; SCHMIDT-THOMÉ, 1968; 1972; WUNDERLICH, 1966; 1968) and East Germany (KETTNER, 1958; KRAUS, 1959; HOHL, 1971).

For all intents and purposes NOPCSA (1927a) was correct when he claimed that his model of orogeny and magmatism is new. There are several reasons why this model was not accepted by other authors. The paper appeared in a Hungarian version and in a German version in the same journal (Földtani Közlöny) which was not widely read outside of Hungary. Only a short version appeared in French in the memoirs of the International Geological Congress in Madrid (1928d) (see KUBACSKA, 1945). NOPCSA was never regarded as an authority on theoretical tectonics. Additionally it seems, at least for German literature, that in the 1930s continuous production of new geotectonic hypotheses which was so characteristic for the 1920s had come to a halt. KIRSCH, AMPFERER, SCHWINNER, STILLE and many others continued to propose their models but no new author appeared on the stage.

WEGENER in the last (fourth) edition of his book (1929) did not mention NOPCSA, for two possible reasons. First, he got the paper too late, since it probably accompanied NOPCSA's letter of Aug. 23, 1928 (reprinted in KUBACSKA, 1945). Second, WEGENER was not interested in the orogenetic and magmatic consequence of his theory. He quoted SCHWINNER (1920; and also KIRSCH, 1928) only with the idea that radioactivity could be the source of energy for plate movement, but thought that it was too premature to decide.

We skip NOPCSA's "Glossen zu E. HAARMANN's Oszillations-Theorie" (1932a). It is a very interesting polemical paper but does not display too much of NOPCSA's own model.

From KUBACSKA (1945) we know how much work NOPCSA spent on his "Zur Geschichte der Adria" (1932b) and how important this project was to him. In a very extensive review of paleontological, regional geological, biogeographical, gravimetric and seismic data NOPCSA showed that the Adriatic See is not a geosyncline but a submerged craton (called "Adriatis"), namely a promontory of the African craton. This model is now generally accepted (CHANNELL et al., 1979). CHANNELL et al. (1979) show that the "Adriatis" (or "Adria") problem dated back to SUESS (1883) and they mention NOPCSA's paper but misrepresent his work by not pointing out that he was an adherent of contineta! drift.

In his last paper which appeared posthumously in England (1934), NOPCSA developed a unified picture of global tectonics and paleogeography which he used as the basis for discussion of the paleobiography of fossil reptiles and Stegocephalia. After he had submitted the English paper, he wrote a German version of his global tectonic concepts and sent it to Centralblatt six weeks before his death.

NOPCSA gave simple but convincing data on paleobiogeography, paleoclimatology and the distributions of orogenies and Carboniferous glaciation to demonstrate that one has to accept continental drift. He avoided introducing WEGENER's theory in a dogmatic way. It is an important addition to his magmatological model of 1927 that he stated (1934, P. 108): "It seems likely that a drifting asunder of land-masses would always be accompanied by eruptions of an Atlantic (basaltic) type. Such a combination... is going on at the present in Great African Rift Valley, on the borders of the Red Sea, and is beginning in the Mediterranean. It is curious that at the beginning of such a process (for example in the African Rift Valley and the Jordan Valley) negative gravity anomalies persist, but that they change later on to positive anomalies (as in the Red Sea and in the Mediterranean)." NOPCSA referred to HOLMES (1931) and pointed out that movement of continental land-masses is feasible because of the possibility of the presence of deep-lying currents. We will not discuss the many data and arguments which NOPCSA used for reconstructing plate movements. It suffices to mention that he criticised WEGENER (1929) and other authors for assuming that continetal blocks drift parallel to each other. Rather, he pointed out, one has to assume rotations and not carry the fitting of the continents according to their outlines too far (as WEGENER had done) because during drifting and rotation, the outlines of the continental blocks are modified. The model which NOPCSA developed is highly speculative (which NOPCSA would probably easily have admitted). He searched for a picture of the structure of the Earth and its development which is as highly patterned and regular as possible. He quoted attempts in the same direction by earlier authors but he went much further than they. In order to understand the current structure of the crust, the Atlantic first must be closed to reveal two orogenetic belts both of which have the size of great circles. These are the equatorial belt, which can be traced not only from Spain to East Asia, but also across the Pacific to Peru and from there back to Spain, and the longitudial belt, again a great circle, which surrounds the Pacific. Local disturbances in the direction and structure fo both belts are explained by local geological conditions. The significance of the belts is shown by magmatism but also by the distribution of earthquakes. A special feature of the longitudinal belt is festoon-shaped island arcs on both sides of the Pacific which all have an eastward convexity. As both orogenetic belts formed since the middle Mesozoic, it is not surprising that the equatorial arc coincides directly with the Jurassic equator and that the northern end of the longitudinal belt is the Jurassic North Pole. If we go back 220 million years, we find in the Variscian (late Paleozoic) mountains traces of two belts roughly 40°–50° north and south which run parallel to the equator. Very small traces are left of a longitudinal Variscian belt. Of the Caledonian orogeny another 220 million years back, we find only parts of a mountain belt which originally probably formed a longitudinal belt. The distribution of glaciations throughout the Phanerozoic enhances the regularity of this pattern. Four factors are responsible for this development of the crust:

1. An eastward force which formed the longitudinal belts with their festoons. Its source is probably the differential rotational velocity of the different layers of the Earth.
2. The high rotational velocity of the Earth which by the action of centrifugal force produced the two Variscian belts at middle latitudes. Later a lower rotational velocity of the Earth together with cosmic factors (gravity of Moon and Sun) formed the Alpine equatiorial belt by compressing action of the centrifugal forces.
3. A migration of the poles which deforms the rotation-elipsoid and which has strongest effects on those meridians on which they migrate.
4. Unknown, but intensive forces (among others also "Polflucht?"), which lead to the breaking up of old sialic blocks.

It is not necessary to discuss the details of this model. Attempts to pack all details of the Earth's history into one simple system were made before NOPCSA and after him (GREENE, 1982). Many of his results and arguments of details of plate movement sound very modern. In contrast to the majority of professional geologists, NOPCSA was an uncompromising "continental drifter" and he always fascinates by the creativity of his ideas and by the fact that he could bring together data which hitherto had been seen in isolation. He must have known AMPFERER's Unterströmungstheorie but he never commented on it. He was well aware of HOLMES' and KIRSCH's ideas of radioactivity as a motor for crustal movement but unfortunately did not see the possibilities of this model and took recourse to ad hoc explanations like "Polflucht" and centrifugal force.

In a very important contribution, SENGÖR (1982) discusses the 1920–1950 schools of thought in global tectonics. He shows that the distinction between "fixists" and "mobilists" does not pinpoint the real issues between the different schools of thought. Issues which characterize the (fixist) "KOBER-STILLE school" are antiuniformitarianism, catastrophism and a belief in an orderly, regular Nature (hence the search for regular tectonic cycles, for regular intervals between glaciations, etc.). The mobilistic "WEGENER-ARGAND school" on the other hand had a strong uniformitarian tendency and believed in an inherently irregular Nature, in which probability rather than determinism was believed to be a realistic approach. SENGÖR shows that, despite the fact that he was a fixist and accepted contraction theory (see also GREENE, 1982), SUESS' uncompromising uniformitarianism made him a predecessor of the WEGENER-ARGAND school. He not only paved the way for the nappists in the last quarter of the 19th century, but also for the mobilists in the early 20th century.

Despite the fact that no documents are known which illuminate SUESS's influence on NOPCSA, SENGÖR's evaluation of SUESS contributes much to an understanding of NOPCSA's ideas on theoretical geology. NOPCSA had no problems accepting the nappist model and continental drift, making very fruitful use of both theories. However, he preferred the determinism which characterized the KOBER-STILLE school (which began in the early 1920s) to the indeterminism of the WEGENER-ARGAND school. It is perhaps not by coincidence that this very last paper tried to develop a highly ordered picture of the history of the Earth which looks familiar if one knows STILLE's work, but which would never have been acceptable for the WEGENER-ARGAND school.

11. Conclusions

Judging from what we know about his life and what can be gleaned from his works, NOPCSA as a scientist is somewhat of a paradox. He was the last of a line of Hungarian nobility and hence never knew the need for employment before World War I. He was sent to the Theresianum, like other children of the nobility, to gain a respectable education. However, at this time in his life, NOPCSA broke with tradition. He did not continue on in university with a degree in law, economics or agriculture; rather he furthered himself in natural sciences. Whether this pathway began through his coincidental encounter with dinosaur bones from the family's estate (and then to SUESS) we do not know. Yet it is clear that NOPCSA advanced himself in vertebrate paleontology at his own hands, as SUESS before him had done for himself in geology (GREENE, 1982). At the same time, NOPCSA learned his geology directly from SUESS.

Because of his financial independence, NOPCSA was not forced to seek a scientific education in order to be employed. An autonomous career in vertebrate paleontology was one of his choosing, and in the days before World War I, he felt free to move to Vienna, with its important resources, rather than live on his Hungarian estate. His heterodox life style and behavior as a scientist can also be attributed to NOPCSA's fortunes. Because he did not depend on the hierarchically structured and constraining university system, his attitudes and enterprises could remain relatively uncompromising and his behavior bordering on the arrogant. Yet to characterize NOPCSA as arrogant is to overlook the obvious problem of combining in one person a high level of intelligence and creativity not often tempered with the ability of self-criticism. NOPCSA's studies in tectonic geology, evolutionary biology, paleobiogeography and sexual dimorphism prove his ability to intelligently discover problems and solve them in remarkable ways. This skill seems to have been lacking among many of NOPCSA's contemporaries. Yet, in retrospect, NOPCSA sometimes failed to ponder the overall feasibility of his hypotheses and arguments. Nor did he seem to care much for selling his ideas; he often did not think very highly of the general readers of his papers. The inability to criticize his own work acted both against and for NOPCSA. Against because of outlandish and easily falsified ideas which he presented on paper; and for, because he excelled at assembling disparate ideas into new frameworks. As such, NOPCSA was one of the first great theorists in vertebrate paleontology and made many noteworthy theoretical contributions in geology and evolutionary biology.

NOPCSA's work was most often accepted only if it was descriptive (viz. his dinosaur and geological work); only some more esoteric studies were not purposefully neglected in German-speaking nations and elsewhere. Indeed, he was invited to England on several occasions to study and deliver talks on dinosaurs and his travels.

For many of his readers of the last 30 years, primarily among English-speaking workers and also due in large part to a one-sided account of NOPCSA's life by EDINGER (1955), repeated by COLBERT (1968), NOPCSA is known primarily for his heterodox behavior. (Without a doubt, NOPCSA contributed in many ways to his own unusual mystique). We argue here that he clearly was no exotic nor a complete outsider to vertebrate paleontology of the early 20th century. Because he was very well read and eclectic in his work, he contributed vast amounts of primary literature and synthetic views on theoretical tectonic geology, neo-Lamarckian evolution and paleobiology of reptiles. Also throughout most of his career, he focused his attention on the conflict of maintaining broad scientific perspectives in the face of the ever-increasing subdivision of scientific disciplines. He spoke out loudly for tearing down the boundaries and filling unoccupied interstices between disciplines: his specialist versus generalist presentation in Budapest (1928b). Only through maintaining a manysided theoretical view into which many seemingly unrelated phenomena come to play could important issues be settled (viz. his work on tectonics and biogeography). To continually subdivide science is to continually lose the connections among associated bits of knowledge. Indeed, NOPCSA's overall research programme was not so much the tackling of large empirical problems or the development of an encompassing theory. Nor was he simply or strictly a solver of evolutionary, paleontological or geological riddles. Rather, it seems that the overall purpose to his work was to stress the bringing together of facts and events which escape the perspective of the specialist. NOPCSA is perhaps the best remembered for campaigning for a new eclectic and synthetic intellectual behavior.

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