Supernumerary teeth in *Lynx lynx* and the irreversibility of evolution

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(With 1 figure in the text)

Supernumerary dental elements have been reported in *Lynx lynx* by several authors. These
features have been given different evolutionary interpretations by different commentators. I
note here that, since these features are absent in the plesiomorphic sister-groups of *L. lynx*, they
represent a true evolutionary reversal. If they were simply a retention of an evolutionarily older
phenotype, we should expect to see them developed in at least one plesiomorphic sister-group.
Such development of a previously hidden character can occur if it is genetically linked to features
selected for, until it becomes phenotypically expressed, whereupon selection can act on the
character itself. Since Dollo's law, which is the theoretical issue behind the present discussion,
is not a law, but a rule, and, like all rules based on probabilities, we should expect to find
exceptions in the fossil record. Such exceptions are not rare, but few are as spectacular as the
present one, in which the redeveloped feature is at least phenotypically identical with one which
has been lost in the Felidae since the Miocene.

Contents

Introduction

The presence of supernumerary dental elements in *Lynx lynx* has been the subject of some
discussion since it was shown by Kurtén (1963) that these elements do not occur merely as
individual anomalies in the dentition of this species, but form a part of its normal dental
variability. The presence of supernumerary elements as a normal rather than anomalous com-
ponent of the dentition of *L. lynx* (when assessed over an entire population) has been considered
by some authors (Kurtén, 1963; Shishkin, 1968; Werdelin, 1981) to be a counter-example to the
'law of irreversibility of evolution', popularly known as 'Dollo's law'. In a recent contribution,
Kvam (1985) has challenged this interpretation in an attempt to bring the phenomenon into line
with the neo-Darwinian synthesis as propounded by, among others, Mayr (1974). I believe

that he has not sufficiently considered the phylogeny of *Lynx*, and that the argument includes misconceptions about both natural selection and evolutionary reversals.

Phylogeny of *Lynx*

Efforts have been made by several authors to clarify the phylogenetic relationships within the genus *Lynx* Kerr, 1792 (Kurtén, 1957a, 1978; Matjuschkin, 1978; Werdelin, 1981, 1985; Kurtén & Werdelin, 1984). In these studies, a certain concensus has been reached concerning the number of species within the genus, and their interrelationships. For example, the Caracal or Desert lynx, *Caracal caracal* (Schreber, 1775), must be excluded from *Lynx*, a result supported by the immunological work of Collier & O'Brien (1985). The species *Lynx canadensis* Kerr, 1792 is recognized, although it must be considered to be very close to *L. lynx*, (Linnaeus, 1758), its putative ancestor (Werdelin, 1981; Pulliainen, 1981). The species *Lynx pardinus* (Temminck, 1824) is also clearly valid and shares with the two previously mentioned species the common ancestor *Lynx issiodorensis* (Croizet & Jobert, 1828) (Kurtén, 1978; Werdelin, 1981). The specific and generic identity of *Lynx rufus* (Schreber, 1777) is also clear, but its phylogenetic status is more equivocal. Werdelin (1981) suggested that this species forms the sister group of *L. pardinus + L. lynx + L. canadensis*. One of the points cited in favour of this hypothesis was the presence of *L. issiodorensis* in the Pleistocene of North America (Schultz & Martin, 1972). This record has since been shown to pertain to '*Felis*' *rexroadensis* Savage, 1959 (Werdelin, 1985), a species which, despite the arguments of Kurtén (1957a) and Glass & Martin (1978), cannot at present be included within the genus *Lynx* (Werdelin, 1981, 1985). There is thus no longer support in the fossil record for Werdelin's (1981) hypothesis concerning the phylogenetic status of *L. rufus*, and because the neontological data are equivocal at present, it cannot be determined whether *L. issiodorensis* or *L. rufus* is the sister group of all other *Lynx*. This leaves us with the phylogeny of *Lynx* as depicted in Fig. 1.
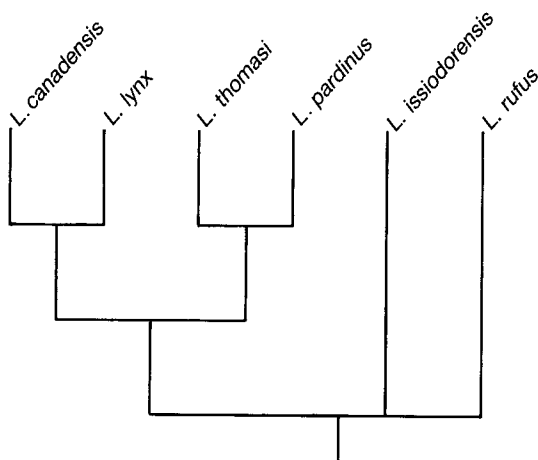

FIG. 1. Cladogram of the genus *Lynx*. Based on Kurtén, 1978; Geraads, 1980; Werdelin, 1981, 1985 and Collier & O'Brien, 1985.

The relevant characters

Only those characters of immediate relevance to the present topic, i.e. characters showing a so-called 'reversal' in evolution will be considered herein. Foremost among these is, of course, M_2, the presence of which in *L. lynx* formed the foundation for the discussion by Kvam (1985). The frequency of expression of this tooth differs between populations of *L. lynx*. It has been variously given as 10 % (Kurtén, 1963), 9·8 % (Hell, 1966), 3·4–5·5 % to 25–27 %, depending on region (Matjuschkin, 1978) and 21 % (Dobrinskij & Malafev, 1975, cited in Matjuschkin, 1978). Most recently, the frequency of M_2 in Norwegian *L. lynx* was examined by Kvam (1985), who found this tooth to be present in 8·7 % of his specimens. In other species of *Lynx*, M_2 is very rare. The only occurrence I have seen reported is in one among nearly 2000 individuals of *L. rufus* studied by Manville (1963). In other felids, M_2 is also exceedingly rare. In only a few instances has this tooth been reported (Colyer, 1936). The only instance which I have personally observed is the unilateral (left side) presence of M_2 in a specimen of *Herpailurus yagouaroundi* from Brazil, RM343, Swedish Museum of Natural History.

The other supernumerary element in the dentition of *L. lynx* is dp^2, which is present in a small fraction of mainly juvenile individuals. Judging by the data presented by Kvam (1985), the presence in a few adults of dp^2 appears to be a developmental anomaly, i.e. the retention of a juvenile character into later ontogenetic stages. This can be a powerful evolutionary mechanism (cf. Gould, 1977), but does not constitute a re-evolved character in the sense that I wish to use this term here. In addition, there is some confusion in the literature concerning whether the dp^2 or P^2 is involved (cf. Kvam, 1985). Finally, this tooth is generally lost and the alveolus closed during the adult life of the individual. This would tend to lower its apparent incidence in fossil specimens and thus perhaps create a spurious impression that it has become more common in *L. lynx* than in *L. issiodorensis*. For these reasons, I will not consider this character further in the present discussion.

In addition to the afore-mentioned characters, Kurtén (1957a, 1963) has documented the re-development of the metaconid-talonid complex in *Lynx*, from its near complete absence in *L. issiodorensis* (Kurtén, 1963, fig. 1b, c), to the presence of a small metaconid and talonid (Kurtén, 1963, fig. 1g) closely resembling those of early felids such as *Pseudaelurus* (Kurtén, 1963, fig. 1a). This change is important, as it shows that the re-emergence of M_2 is part of a complex pattern of evolutionary change in the dentition of *L. lynx*.

These characters form the factual basis upon which arguments concerning discussions of evolutionary reversals in *Lynx* must be based. Their relative development in the relevant taxa is summarized in Table I.

Selection

Kvam (1985) notes that, according to the generally accepted version of the neo-Darwinian synthesis, selection acts at the level of the individual, a matter which has been the subject of some debate over the past decades (e.g. Williams, 1966; Dawkins, 1976; Stanley, 1979). In particular, selection acts on the phenotype, not the genotype (*pace* Dawkins, 1976). I agree fully with this point of view, if not necessarily as a general statement, then at least in the present case. Whatever the selection pressure that may have acted on the dentition of *Lynx* during the Pleistocene, it acted directly on the observable phenotype and not on phenotypically inactive genetic traits. This does not mean that these inactive traits could not have been re-activated by

TABLE I

*Relative development in various species of **Lynx** of the characters discussed in the text*

	Character		
Species	Presence of M_2	Development of metaconid-talonid	n
Lynx lynx	yes—see text	strongly developed	150
L. canadensis	none known	weak development	53
L. pardinus	none known	weak development	63
L. rufus	very rare abnormality	not developed	145
L. issiodorensis	none known	variable depending on evolutionary stage	≈ 50
L. thomasi	none known	weak development	1
Other felids	very rare abnormality	not developed or weak development	

the existing selection pressure, however, such an argument fails to take into account two points: limits to the modification of existing features (i.e. evolutionary constraints) and possible linkage between phenotypically active and inactive traits. In the present instance, the first point means that there may be a limit to the possible enlargement of M_1, the second that such enlargement may, through linkage, raise M_2 above the threshold of phenotypic expression (Kurtén, 1953) and thereby to the point at which it can be selected for (note that I am not suggesting here, as Kvam [1985] does, that the presence of M_2 is due entirely to linkage with features that are positively selected for, only that such linkage may make it possible for selection to act on the previously hidden character).

Character evolution in *Lynx*

If we pass now from hypothetical possibilities to the case at hand, we may note that, just as Kvam (1985) points out, if there was selection pressure for increased length of the molar region in *Lynx*, it is more likely that M_1 would increase in length rather than M_2 being redeveloped. This is in fact what has happened in the evolution of *Lynx*. The M_1 is significantly longer relative to P_4 in both *L. lynx* and *L. pardinus* than in *L. issiodorensis* (Tables II and III). The observed facts thus agree exactly with the argument presented by Kvam (1985). I suggest, however, that the selection pressure for an enlarged molar region proceeded further in *L. lynx* than an enlargement of the M_1 alone could accommodate. Through linkage with M_1 in the molarization field

TABLE II

*Index of relative length of P_4 and M_1 in various species of **Lynx**.*
n = number of specimens, S.D. = standard deviation. All are
*Recent samples, except **L. issiodorensis** and **L. thomasi***

Species	n	Mean	S.D.	Range
Lynx lynx	23	80·8	2·97	76·3 – 87·1
L. canadensis	29	83·8	3·53	78·0 – 92·1
L. pardinus	15	78·6	3·88	71·4 – 86·3
L. rufus	26	85·5	4·63	74·4 – 96·2
L. issiodorensis	14	86·3	3·82	78·3 – 93·6
L. thomasi	1	68·5		

TABLE III

*Significance tests of indices of relative length of P_4 and M_1 shown in Table II. Values of **t** (Sokal & Rohlf, 1981, equation 9·2, p. 226) are given; values significant at the 1 % level are shown in boldface*

	canad.	pardi.	rufus	issio.	thoma.
Lynx lynx	**3·260**	1·977	**4·166**	**4·900**	1·365
L. canadensis		**4·479**	1·541	2·119	1·207
L. pardinus			**4·864**	**5·380**	0·650
L. rufus				0·552	0·778
L. issiodorensis					1·178

(Butler, 1939), M_2 may in some individuals have reached the level of phenotypic expression, and these two factors taken together would lead to selection for the presence of M_2.

This hypothetical scenario shows that there is nothing in the re-evolution of the M_2 in *Lynx* which is intrinsically incompatible with current views of evolution by natural selection. Let us now consider the situation in terms of the phylogenetic history of *Lynx*. Study of the cladogram (Fig. 1) and Table I shows that none of the sister groups of *L. lynx* has the character state 'M_2 present'. This fact would by itself lead us to suspect that the presence of this character state in *L. lynx* is a case of evolutionary reversal. If the character state were due merely to retention of an earlier state, we would expect its presence, at least in the most primitive member of this monophyletic group, in this case either *L. issiodorensis* or *L. rufus*. In the first of these two species one might, if this tooth is lost soon after eruption, make a case for the non-presence of M_2 being due to preservational bias. This seems not to be so, however. In the specimen of *L. lynx* illustrated by Kurtén (1963, fig. 2), M_2 is quite worn through occlusion with P_4 and M_1, indicating that some time has passed since the tooth erupted. In addition, the data presented by Kvam (1985, table II) show that, in his material, M_2 is present in approximately the same frequency in all age groups. Curiously, Kvam ignores his own data in asserting (1985: 21) that 'dp^2 and M_2 seem to be lost at an early stage after eruption'. Whilst this is true of dp^2, it is not of M_2. It is not easy to determine the exact sample size of *L. issiodorensis* available (Croizet & Jobert, 1828; Fabrini, 1896; Teilhard & Leroy, 1945; Viret, 1954; Kurtén & Werdelin, 1984), as it may in some instances be difficult to see if M_2 might have been present or not. However, this sample size is approximately 50, and one would expect, if M_2 were as frequent in this species as in *L. lynx*, to find some evidence of its presence. The probability of *not* finding an M_2 in *L. issiodorensis* given these circumstances is approximately $(9/10)^{50}$, or 0·0052. However, no trace of M_2 is seen in any of these specimens. Whilst this in no way constitutes absolute proof that M_2 was not present in *L. issiodorensis*, it is at least strong corroboration of this hypothesis. Presence of M_2 in frequencies as low as that of *L. rufus* (< 0·05 %) would not be detected in the presently available samples of *L. issiodorensis*, but I think it must be argued that a frequency this low is attributable to individual abnormality rather than being characteristic of the species. I thus consider it clearly established that M_2 was, in fact, not present in *L. issiodorensis*. The conclusion that M_2 has re-evolved in *L. lynx* is inescapable.

The same arguments apply, with some slight modification, to the redevelopment of the metaconid-talonid complex in *L. lynx*. The scenario has been presented in detail by Kurtén (1957a, 1963) and will not be repeated here. The difference between this case and the case of M_2 is that here the character in question is present to some degree in all species of *Lynx* except *L. issiodorensis* and *L. rufus*, although it reaches its extreme development in *L. lynx*. This actually strengthens the

case for evolutionary reversal, as we are here dealing with a multi-state situation in which a character evolves from non-presence (*L. issiodorensis*) over weak development (e.g. *L. pardinus*) to strong development (*L. lynx*). A feature of special interest is that, if Pulliainen (1981) and Werdelin (1981, 1985) are correct in believing *L. canadensis* to have evolved from *L. lynx* fairly recently, then there must be yet another reversal of this character in the evolution of *Lynx* as the metaconid-talonid complex goes from strong presence in *L. lynx* to weak presence in *L. canadensis*.

Evolutionary reversals

I hope to have shown in the previous section that the presence of M_2 and the metaconid-talonid complex of M_1 should be regarded as true reversals of long-standing evolutionary trends within the Felidae. In the present section, I wish to discuss evolutionary reversals in general and to show that Dollo's law is irrelevant to current evolutionary thought.

First of all, it should be noted that Dollo's law in the form in which it is given by Abel (1929, cited by Kvam, 1985), namely 'An organ which has been lost in the course of phylogeny will never reappear in its original form though it may be replaced by a similarly functioning but non homologous anatomical structure', cannot be falsified and is consequently not a scientific statement at all (Popper, 1959). In theory, it should be possible to determine whether an original and a re-evolved anatomical structure are homologous, though this would involve identification of the gene-coding for the two features. Traditional criteria of homology are insufficient, as it can generally be claimed by adherents to Dollo's law that the re-evolved character is really a newly evolved character, merely analogous with the old one. In the present case, it might be argued, for instance, that the metaconid of *L. lynx* is really a newly evolved pseudo-metaconid, not at all homologous with the metaconid of *Pseudaelurus*. Such recourse to the genotype, although beyond present techniques, may become possible in the future. However, this will still only help under the rather special circumstance where the carrier of the plesiomorphic version of the structure and the carrier of the secondarily evolved apomorphic version are both extant. When dealing with fossil organisms, there is no recourse to the genotype, and thus no possibility of rigorously falsifying Dollo's law.

A falsifiable formulation of Dollo's law could certainly be presented. However, a more important point is that, as Popper (1979) notes, no law is without exceptions, although the probability of finding one may vary greatly between laws. Thus, we can expect, on the basis of the law of gravitation, that every apple that detaches from its tree will fall downwards (though not all will strike brilliant scientists on the head). The probability of an exception is here so small that if one did occur the foundations of science would need to be re-examined. The same would hold for some other causal laws of physics. With many other laws the situation is different; the probability of an exception is relatively high, and examples should be expected. In biology, most such laws are termed 'rules', e.g. Bergmann's rule and Cope's rule (Rensch, 1960). And so it is with Dollo's law: exceptions to it are many. Some are trivial, and may be argued not to belong in this category at all, such as cases of size fluctuations in Pleistocene mammals (Kurtén 1957*b*, 1960; Nelson & Semken, 1970). Others are minor but real, such as that described by Gingerich (1976, 1977) in the Plesiadapidae. Still others are more spectacular, such as that discussed herein, or the dental evolution of dwarf elephants (Maglio, 1972), and these tend naturally to be cited on more occasions.

Finally, I should like to point out that the neo-Darwinian synthesis is silent on the subject of

Dollo's law. There is nothing intrinsic to this theory which precludes evolutionary reversals, and I hope to have shown above that the recurrence of lost characters is entirely compatible with a neo-Darwinian evolutionary scenario, despite the fact that one cannot select for what is not there. That which is not there can be genetically linked to that which is.

Summary

Kvam (1985) reports the presence of M_2 in *Lynx lynx* in frequencies consistent with previous studies. Contrary to earlier commentators (Kurtén, 1963; Shishkin, 1968; Werdelin, 1981), he does not consider this a case of evolutionary reversal, inconsistent with Dollo's law or with the neo-Darwinian synthesis as interpreted by Kvam (1985). Consideration of the mode of action of natural selection in conjunction with a study of the phylogenetic relationships within the genus *Lynx* shows that the observed facts are consistent with an evolutionary reversal. The interesting feature of this reversal is not so much its morphological details, but rather the time elapsed since the last previous presence within the Felidae of a character at least phenotypically homologous with the one under discussion.

All laws of nature, including Dollo's, are probabilistic in nature, and exceptions must be expected and allowed for. That evolution should be irreversible is not a necessary consequence of the neo-Darwinian synthesis, but is rather due to the way in which information is accumulated in the genome and expressed through developmental pathways (Riedl, 1978). The viewpoints of Kurtén (1963) and Werdelin (1981) on the presence of M_2 in *L. lynx* are therefore not opposed to the neo-Darwinian synthesis, nor were they meant to be.

REFERENCES

Abel, O. (1929). *Paläobiologie und Stammesgeschichte.* Jena: Gustav Fischer Verlag.

Butler, P. M. (1939). Studies of the mammalian dentition. Differentiation of the post-canine dentition. *Proc. zool. Soc. Lond.* **109B:** 1–36.

Collier, G. E. & O'Brien, S. J. (1985). A molecular phylogeny of the Felidae: Immunological distance. *Evolution, Lawrence, Kans.* **39:** 473–487.

Colyer, J. F. (1936). *Variations and diseases of the teeth of animals.* London: Bale.

Croizet & Jobert (1828). *Recherches sur les ossemens fossiles.* Paris.

Dawkins, R. (1976). *The selfish gene.* Oxford: Oxford University Press.

Dobrinskij, L. N. & Malafev, J. M. (1975). Contribution to the epigenetic polymorphism of the lynx of the central Ural area. In *Problems of soil science and protection of the environment*: 57–59. Irkutsk. [In Russian.] (Cit: Matjuschkin, 1978.)

Fabrini, E. (1896). La lince del Pliocene Italiano. *Palaeontogr. ital.* **2:** 1–24.

Geraads, D. (1980). Un nouveau félide (Fissipeda, Mammalia) du Pleistocène moyen du Maroc: *Lynx thomasi* n. sp. *Géobios, Lyon* **13:** 441–444.

Gingerich, P. D. (1976). Cranial anatomy and evolution of early Tertiary Plesiadapidae (Mammalia, Primates). *Pap. Paleont. Mus. Paleont. Univ. Mich.* No. 15: 1–140.

Gingerich, P. D. (1977). Patterns of evolution in the mammalian fossil record. In *Patterns of evolution*: 469–500. Hallam, A. (Ed.). Amsterdam: Elsevier.

Glass, G. E. & Martin, L. D. (1978). A multivariate comparison of some extant and fossil Felidae. *Carnivore* **1:** 80–87.

Gould, S. J. (1977). *Ontogeny and phylogeny*. Cambridge, Mass.: The Belknap Press of Harvard University Press.

Hell, P. (1966). Polydontie beim Europäischen Luchs *Lynx lynx* L. *Z. Säugetierk.* **31:** 392–393.

Kerr, R. (1792). *The animal kingdom, or zoological system of the celebrated Sir Charles Linnaeus; class I, Mammalia.* London: Gmelin.

Kurtén, B. (1953). On the variation and population dynamics of fossil and recent mammal populations. *Acta zool. fenn.* **76:** 1–122.

Kurtén, B. (1957a). A note on the systematic and evolutionary relationships of *Felis teilhardi* Pei. *Vertebr. palasiat.* **1:** 123–128.

Kurtén, B. (1957b). The bears and hyenas of the interglacials. *Quaternaria* **4:** 1–13.

Kurtén, B. (1960). Chronology and faunal evolution of the earlier European glaciations. *Comment. biol.* **21:** 1–62.

Kurtén, B. (1963). Return of a lost structure in the evolution of the felid dentition. *Comment. biol.* **26:** 1–12.

Kurtén, B. (1978). The lynx from Etouaires, *Lynx issiodorensis* (Croizet & Jobert), late Pliocene. *Ann. zool. fenn.* **15:** 314–322.

Kurtén, B. & Werdelin, L. (1984). The relationships of *Lynx shansius* Teilhard. *Ann. zool. Fenn.* **21:** 129–133.

Kvam, T. (1985). Supernumerary teeth in the European lynx, *Lynx lynx lynx*, and their evolutionary significance. *J. Zool., Lond.* **206:** 17–22.

Linnaeus, C. (1758). *Systema naturae.* 10th edn. Stockholm.

Maglio, V. J. (1972). Evolution of mastication in the Elephantidae. *Evolution, Lawrence, Kans.* **26:** 638–658.

Manville, R. H. (1963). Dental anomalies in North American lynx. *Z. Säugetierk.* **28:** 166–169.

Matjuschkin, E. N. (1978). Der Luchs *Lynx lynx*. *Neue Brehm Büch.* No. 517: 1–160.

Mayr, E. (1974). *Populations, species and evolution.* 3rd edn. Cambridge, Mass.: The Belknap Press of Harvard University Press.

Nelson, R. S. & Semken, H. A. (1970). Paleoecological and stratigraphic significance of the muskrat in Pleistocene deposits. *Bull. geol. Soc. Am.* **81:** 3733–3738.

Popper, K. R. (1959). *The logic of scientific discovery*. London: Hutchinson.

Popper, K. R. (1979). *Objective knowledge. An evolutionary approach.* Revised edn. Oxford: Oxford University Press.

Pulliainen, E. (1981). Winter diet of *Felis lynx* L. in SE Finland as compared with the nutrition of other northern lynxes. *Z. Säugetierk.* **46:** 249–259.

Rensch, B. (1960). The laws of evolution. In *Evolution after Darwin* **1:** 95–116. Tax, S. (Ed.). Chicago: University of Chicago Press.

Riedl, R. (1978). *Order in living organisms*. Chichester: John Wiley & Sons.

Schreber, J. C. D. von (1775). *Die Säugethiere in Abbildungen nach der Natur, mit Beschreibungen.* Erlangen (1775–92).

Schultz, C. B. & Martin, L. D. (1972). Two lynx-like cats from the Pliocene and Pleistocene. *Bull. Univ. Neb. St. Mus.* **9:** 197–203.

Shishkin, M. A. (1968). Morphogenetic factors and the irreversibility of evolution. *Paleont. J.* **3:** 293–299.

Sokal, R. R. & Rohlf, F. J. (1981). *Biometry*. 2nd edn. San Francisco: Freeman.

Stanley, S. M. (1979). *Macroevolution*. San Francisco: Freeman.

Teilhard de Chardin, P. & Leroy, P. (1945). Les félidés de Chine. *Publ. Inst. Géobiol., Pékin.* **11:** 1–58.

Temminck, C. J. (1824). *Monographies de mammalogie.* Paris.

Viret, J. (1954). Le loess à bancs durcis de Saint-Vallier (Drôme) et sa faune de mammifères Villafranchiens. *Nouv. Arch. Mus. Hist. nat. Lyon* No. 4: 1–200.

Werdelin, L. (1981). The evolution of lynxes. *Ann. zool. fenn.* **18:** 37–71.

Werdelin, L. (1985). Small Pleistocene felines of North America. *J. Vert. Pal.* **5:** 194–210.

Williams, G. C. (1966). *Adaptation and natural selection.* Princeton, N. J.: Princeton University Press.