A 34-year study (1966-2000) of the lizards and snakes of the New England region of New South Wales yielded 14 species of geckos, 4 of pygopodids, 8 of dragons, 3 of goannas, 47 of skinks, and 30 of snakes, for a total of 106 species. Four additional species reported by Swan (1990), and an additional one from the Atlas of NSW Wildlife brings the total known squamatan fauna of New England to 111 species. Most terrestrial families of squamates in New England represent 10-15% of the total Australian species. The exceptions are the families Elapidae (26%) and Colubridae (18%). Generic representation is higher and more variable. A fifth of the species are widespread. Other species are predominantly separated into eastern and western faunal groups. In some species the Great Dividing Range coincides with east-west distributional boundaries. In others, the borders of the distributional range lie one side or the other of this topographical feature. In both western and eastern groups, there are species associated mainly with either the northern or southern quadrants; otherwise distributions of only a few species are oriented with respect to the north-south axis. There were no strictly central species. Some species are represented by only one or a few records and the full extent of their distributions may not be appreciated, or they may be sparsely distributed, rare, or cryptic. A number of species were distributed randomly with regard to particular environmental attributes; these were unlikely to be affecting distribution within New England. Where correlations did exist, causal effects could only be hypothesised, but optimal habitats could be defined by over-representation in localities with particular levels of elevation, rainfall, or temperature, or characterised by certain types of vegetation, rock or soil.

An initial paper of the faunal survey of New England described the general geography of the area (Heatwole & Simpson, 1986); this was followed by accounts of the gastropods (Simpson & Stanisic, 1986), birds (Ford & McFarland, 1991) and frogs (Heatwole et al., 1995). The present paper reports on the lizards and snakes.

There have been several interpretations of the boundaries of New England (see Lea et al., 1977 and electoral maps). We recognise the boundaries as defined in the previous papers of this series (Fig. 1).

Treatment of the fauna is at the specific level; subspecific designations are not included.

METHODS

In the interests of conservation, we collected only a few voucher specimens of each species from any given area. Nevertheless, over the 34 years of the study (1966-2000) we collected and identified more than 6,000 specimens of snakes and lizards and deposited them in the Australian Museum.

This material was augmented by other herpetological collections in the Australian Museum (up to 2000), and by the holdings of the Museum of Victoria, and the Queensland Museum (both up to 1996). Initially, we eliminated records referring to specimens that had been discarded or lost, or which had deteriorated beyond accurate identification, corrected some misidentifications, and verified or corrected data for unusual specimens such as geographical outliers. After this editing, we relied heavily on the registers of those museums. Especially important has been the progressive upgrading by the Australian Museum of their herpetological collections, whereby incompletely unidentified specimens were identified, previously identified specimens checked for accuracy, nomenclatural changes incorporated, and geographical coordinates and other data verified or corrected.

Taxonomic nomenclature follows that of Cogger (2000) and Cogger et al. (1983), but incorporates recent name changes and generic allocations by King (1983), Wells & Wellington...
A number of surveys and environmental consultancies for specific purposes amassed a corpus of data relating to the New England area. Specimens arising from these studies were deposited in the Australian Museum and automatically became part of our database. In addition, a large number of the records were not based on voucher specimens, but rather upon field identifications of varying reliability. We have not included any sight records in our database but do discuss them below where relevant.

Our final, edited dataset, consisting of our collections plus the other acquisitions of the three museums, is based on more than 12,800 specimens that were collected from the late 19th century to the end of the twentieth century. Using the statistical package, StatView, locality data were formatted for the ArcView Mapping System to produce distribution maps of each species. In this system, multiple records of a given species for a particular locality were grouped as a single entity and latitudes and longitudes from museum records were converted to a decimal degree.

The final edited dataset totalled 4,045 records and comprised 3,175 localities within the boundaries of New England (Fig. 1), and 888 records from sites immediately extralimital (Figs 2, 3-108) that were included for mapping purposes. This has been placed in each of the three museums both as hard copies and CD ROM.

The New England survey of frogs (Heatwole et al., 1995) related species distributions to four environmental parameters: mean daily minimum temperature for July, mean annual rainfall, elevation, and vegetation. Because many squamates behaviourally thermoregulate, are cryptic, or are substrate-dependent in various ways, an enlarged set of parameters was employed, including soil type and rock type. Heatwole & Simpson (1986) presented a map of the lithology of New England based on ‘An Atlas of New England’ (Lea et al., 1977). For the present paper an improved map, derived from the New South Wales Department of Mineral Resources 1:25000 Geological map, was used.

The soil map derives from Lea et al., 1977. This was digitised, and the map prepared using the Environmental Research Mapping Program (ERMS) in the Armidale office of the National Parks and Wildlife Service of New South Wales (Ferrier, 1989).

The vegetation map is based on a modification of the classification of vegetation systems for northeastern New South Wales (NSW National Parks and Wildlife Service, 1994). The nine categories of that classification were lumped into three categories: ‘disturbed’ (including pastoral and agricultural land), ‘dry forest and woodland’ and ‘wet forest’ (including rainforest).

New, more detailed maps of elevation, rainfall and temperature were prepared. The Environmental Research Mapping System (ERMS) in the Armidale office of the National Parks and Wildlife Service of New South Wales (Ferrier, 1989) was used to prepare maps of the distribution of soils, and the distribution of various variables.

Long-term monthly means of minimum temperature, maximum temperature, and precipitation were derived by linking a gridded digital elevation model with climate surface models developed by Hutchinson (1989). These
For statistical treatment, the proportion of grids falling into these various categories was calculated separately for each environmental attribute. Then from these proportions, the expected number of grids in each category expected to be occupied by a given species was calculated and the observed values compared to expected values and tested for statistical significance by chi-squared tests, using a rejection level of 5%. These tests were conducted in 1996 on the database available at that time and not recalculated to include the few later acquisitions; only localities located within the boundaries of New England (Fig. 1) were included in the statistical analyses.

For valid statistical testing, no category should have an expected value less than five. Some categories of vegetation, soil type and rock type were sparsely represented in the region and did not meet this requirement. To overcome this, the smaller categories were lumped to raise their collective expected value into the appropriate range. Some environmental parameters had more disparate frequencies of categories than did others. For example, in vegetation systems, rainforest and other wet forest occupy only a small proportion of the total area of New England, and there were relatively few collecting localities located within it. Nevertheless, it was unrealistic to lump these important habitats with those of a distinctly different character merely in order to allow the mechanics of statistical testing to proceed. For this reason, in order to reach the criterion of an expected value of five for rainforest/wet forest, only species of squamates with a high number of occurrences (N) in New England could be tested. Other parameters, with more uniform frequencies of environmental categories, could be tested for species with a lower N. The minimum values of N for the different environmental parameters after lumping of categories were: Elevation = 28; Rock Type = 34 for four categories (an N of 95 allowed testing of five categories); Maximum Temperature = 36; Rainfall = 46; Soils = 48 for five categories and 80 for six; Minimum Temperature = 49; Vegetation System = 74.

Two examples (Table 1) illustrate the technique. (1) *Eulamprus quoyii* in relation to elevation: this species occurred in 64 grid squares in the study area. Since 26.39% of the grid squares had a mean elevation of 0-700m, if this species were distributed at random with respect to elevation, then it would be expected to occur in 16.89 grid squares at this elevation (26.39% of 64); the
observed value was 11. Similarly expected values were 11.96 for 701-900, 10.42 for 901-1000, 12.2 for 1001-1100, and 12.44 for 1101-1600. The corresponding observed values were: 8, 16, 13 and 16. The chi-square value of the comparison of observed to expected values was 7.414 (0.25>P>0.10). Since P>0.05, *E. quoyii* was considered to be distributed randomly with respect to elevation, within the range of elevations occurring within the study area.

(2) *Ctenotus robustus* in relation to rainfall. The expected (observed) values for the 46 grid squares in which this species occurred was: 4.50 for <700mm rainfall, 14.86 for 700-800mm, 9.17 for 801-900mm, 5.82 for 901-1000mm, 5.43 for 1001-1100, and 6.17 for >1100mm. The respective observed values were 8, 23, 8, 5, 2 and 0. The chi-square value was 15.197 and 0.01>P>0.005 (highly significant). Thus, this species was not randomly distributed with respect to rainfall. Note that the observed values were greater than expected by randomness in the first two categories (<700mm and 700-800mm) and less than expected in all the rest. The optimal habitat for *C. robustus* therefore seems to be the drier parts of the area.

For some species, over-representation occurred only in one category, in other species over-representation occurred over a broader range of values and encompassed several categories.

Copies of the detailed statistical tests, including all observed and expected values, chi-squares and P values, as well as histograms of frequency distributions of environmental parameters, have been placed on file in the Australian Museum and in the Queensland Museum.

Although nearby extralimital localities were plotted on species’ distribution maps, only the localities within the boundaries of the New England region were included in the statistical analyses.

A transparency of the State of New South Wales, with the area of New England delineated as defined in the present study, was produced at the same scale as Swan’s (1990) maps. By overlapping this transparency onto Swan’s maps and comparing them, the species and localities included in his study were detected and compared with ours.

**COVERAGE**

The long duration of this survey allowed opportunity for a comprehensive geographical coverage of the area (Fig. 2). Collections were made throughout the area with no large gaps, although the collecting localities were slightly less densely distributed in the west than elsewhere.

Even with a relatively complete geographic coverage, a distorted picture could be obtained if important habitats were poorly represented. For example, not collecting along streamsides in New England would have failed to reveal the presence of several species. We attempted to cover all habitats. In order to assess the extent to which that attempt was successful, the areas covered by each category of the various environmental parameters was calculated from the computer-generated environmental maps, and the number of collecting sites represented in each category ascertained. For each parameter, the number of collecting sites in a given category was roughly proportional to the representation of that category in the region. Thus, it appears that all recognised habitats were adequately covered.

The seasonal coverage was not as good. Many localities were visited only once. Consequently, if certain species were active only outside that period, they would have been missed.

**OTHER RECORDS FOR NEW ENGLAND**

Swan’s (1990) maps were based partly on records not available to us and they add four species (*Hypsilurus spinespis*, *Tympanocryptis diemenensis*, *Lerista punctatovittata*, *Cryptoblepharus carnabyi*) to the fauna of New England. He reported *Phyllurus cornutus* from the area, but Couper et al. (1993) restricted this species to northeastern Queensland and allocated the New England population to *Saltuarius swaini*. Swan also reported *Ramphotyphlops broomi* from New England but Shea (1995) demonstrated the New England species to be *R. wiedii*. Thus, we have excluded *Phyllurus cornutus* and *Ramphotyphlops broomi* from the list of species from New England.

The Sarah River Survey (Webber & Heatwole, 1991), an action plan for threatened Australian reptiles (Cogger et al., 1993) and the Eastlink Survey of 1995-1997, conducted along a transect through northern New England and southern Queensland (Debus, unpubl. data) yielded no species for the New England squamatan fauna beyond those listed in Table 1 from other sources. The Atlas of NSW Wildlife of (NSW National Parks and Wildlife Service, database of the year 2000) summarised all records from New South Wales, including New England, arising from a
Denisonia maculata, New England fauna; their known ranges are far
from New England. The following species were recorded from New
England only on the basis of field identifications: Phyllurus platurus, Egernia striata, Eualamprus
tympanum, Hemisphaeriodon gerarrdii, all with a reliability index of 4 or 5 (with 1 being most
reliable, 6 least reliable). The last is known
undoubtedly just east of New England and
further investigation may well extend its range
into the region. However, the first three species
almost certainly represent erroneous identifications and we do not consider them part of the
New England fauna; their known ranges are far
removed from New England (Cogger, 2000).

One of the species listed in our database, Denisonia maculata, may be in error. The record
is based on a single specimen from the Australian
Museum (AM R4765) that was later donated to
the Museum of Comparative Zoology at Harvard.
J. Rosado (pers. comm.) indicated that because of
renovations this specimen would be unavailable
for an identity check for at least another year.
Cogger (2000) showed the range of D. maculata
as coastal central Queensland, well beyond the
limits of New England. D. maculata is closely
related to D. devisi and the latter was once
considered a subspecies of the former (Cogger et
al., 1983). D. devisi is one of the species reliably
recorded from New England by the Atlas of NSW
Wildlife (Table 1 and see above) and it is likely
that the purported specimen of D. maculata is, in
fact, D. devisi.

Ctenotus eurydice: This species is now regarded
as an invalid species (Sadler, pers. comm.),
since it cannot be reliably distinguished from C.
taeniolatus, and is therefore excluded from our
data base. The New England specimens of C.
eurydice were SPXEIO13 (NSW Wildlife Survey,
1988), SPXEIOO6 (Atlas of NSW Wildlife)
Neither of them can now be located.

Ge hyra australis: There are three records of this
species from closely adjacent sites in the Moonbi
Ranges near Tamworth, NSW, (AM R29700,
AM R75990, VM D55544). They form a cluster
within a predominantly G. dubia population. The
Australian Museum specimens could not be
located, but that from the Victorian Museum was
initially identified as G. australis by the Acting
Curator of Herpetology, (D.J. Bray), and by one
of the authors (J.de B). The specimen was then
referred to the Australian Museum where it was
identified as G. dubia because of the presence of
an internasal scale, a characteristic of that species
(R.Sadlier, pers. com.). Consequently the three
records of G. australis were transferred to G. dubia.

The reliably known squamatan fauna of New
England therefore consists of (a) our database of
106 species (14 species of geckos, 4 of pygo-
podids, 8 of dragons, 3 of goannas, 47 of skinks,
and 30 of snakes); (b) four additional species (2
dragons and 2 skinks) reported by Swan (1990);
and (c) an additional species based on voucher
specimens from the Atlas of NSW Wildlife
database, for a total of 111 species.

Several more are immediately extralimital and
further collecting may record their presence in
New England. Faunal surveys involving parts of
New England are in progress (e.g., Nandewar
Ranges in western New England; Demon Nature
Reserve on the Timbarra Plateau in eastern New
England). The preliminary lists are subject to
revision and reassessment before they are
permissible for quotation; accordingly, it was not
possible to include information from them in the
present study.

THE REGIONAL FAUNA IN RELATION TO
THE HERPETOFAUNA OF AUSTRALIA

The majority of Australian squamates live in
tropical or arid habitats and are thus excluded
from New England (Cogger, 2000). Overall, 14%
of Australian species of squamates and 47% of
the genera occur in New England. At the specific
level, all Australian families of lizards are similar
in their proportional representation in New
England (12-15% of the total species from
Australia) (Table 2). By contrast, the different
ophidians families, have markedly divergent
proportional representations in New England at
the species level. The Typhlopidae and Boidae
have about the same proportional representation
(10-13%) as the saurian families, whereas the
colubrids and the elapids are unusually well
represented (Table 2).

Generic representation is higher than specific
representation. All Australian monitors belong to
Varanus and consequently New England has a

NEW ENGLAND LIZARDS AND SNAKES
TABLE 1. List of the lizards and snakes known from the New England Region and a summary of their types of distributions. * recorded for the New England region by Swan (1990) but not present in our database; ** recorded in Atlas of NSW Wildlife database, based on a voucher specimen, but not in our database.

Key to symbols indicating distributional pattern within the New England region: U(e)=widespread and evenly distributed; U(p)=widespread but patchily distributed; U(s)=widespread but sparsely distributed; W= mainly distributed in the western part of the area; W(sw)=mainly in the southwestern sector; W(nw)=mainly in the northwestern sector; E= distributed mainly in the eastern part of the area; E(ne)=mainly in the northeastern sector; E(se)=mainly in the southeastern sector; S = mainly distributed in the southern part of the area; R= recorded from less than ten localities in our database.

**LIZARDS**

**FAMILY AGAMIDAE (Dragons)**
- Amphibolurus burnii (Wells & Wellington, 1985): W(nw)
- Amphibolurus muricatus (White, ex Shaw, 1790): U(e)
- Amphibolurus nobbi Witten, 1972: U(e)
- *Hyphython spinipes* (Duméril & Dumeril, 1851): E, R
- Physignathus lesueurii (Gray, 1831): U(p)
- Physignathus tetraporophora (De Vis, 1888): W, R
- Pogona barbata (Cuvier, 1829): W
- Pogona viticeps (Ahl, 1926): W, R
- *Tympanoctyptis diemenensis* (Gray, 1841): S, R
- Tympanoctyptis lineata Peters, 1863: W
- Tympanoctyptis tetraporophora Lucas & Frost, 1895: W, R

**FAMILY VARANIDAE (Monitors or Goannas)**
- Varanus guilorii (Gray, 1838): U(s)
- Varanus iristis (Schlegel, 1839): W(nw), R
- Varanus varius (White, ex Shaw, 1790): W, R

**FAMILY GEKKONIDAE (Geckos)**
- Diploscactus intermedius Ogilby, 1892: W, R
- Diploscactus vittatus Gray, 1832: W
- Diploscactus williamisi Kluge, 1963: W, R
- Gehyra dubia (Macleay, 1877): W
- Gehyra variegata (Duméril & Bibron, 1836): W, R
- Heteronota binoei (Gray, 1845): W
- Oedura leueuertii (Duméril & Bibron, 1836): W
- Oedura monilis De Vis, 1888: W, R
- Oedura robusta Bouleguer 1885: W
- Oedura tryoni De Vis, 1884: W
- Saltuarius swaini (Wells & Wellington, 1985): E
- Saltuarius wyerhba Cooper, Schneider & Covacevich, 1997: E(ne), R
- *Underwoodisaurus mili* (Bory de Saint-Vincent, 1825): W
- Underwoodisaurus sp. (Ogilby, 1892): W

**FAMILY PYGOPODIDAE (Snake-lizards)**
- Delma tincta De Vis, 1888: W, R
- Delma tincta De Vis, 1888: W, R
- Lialis burtonis Gray, 1835: U(p)
- Pygopus lepidopodus (Lacépède, 1804): U(s), R

**FAMILY SCINCIDAE (Skinks)**
- Anomalopus leuckarti (Weinland, 1862): W
- Anomalopus mackayi Greer & Cooper, 1985: W(nw), R
- Anomalopus veregalusii (Duméril & Dumeril, 1852): E, R
- Bassiana platyphra (Peters, 1881): E
- Calyptritis ruficauda Greer, 1983: E
- Calyptritis scutirostrum (Peters, 1873): E(ne)
- Carlia tetradactyla (O'Shaughnessy, 1879): W
- Carlia vivax (De Vis, 1884): U(p), R
- Caulota zia (Ingram & Ehmann, 1981): E, R
- Coenura pustulata (Günther, 1873): E(ne), R
- Cryptoblepharus barnabyi Storr 1976: R
- Cyclodomorphus michaeli Wells & Wellington, 1984: R
- Egeria cunninghami (Gray, 1832): U(e)
- Egeria frerel Günther 1897: E(ne), R
- Egeria major (Gray, 1845): U(s), R
- Egeria mepheii Wells & Wellington, 1984: E
- Egeria modesta Storr, 1968: R
- Egeria satxalitis Cogger, 1960: W, R
- Egeria striolata (Peters, 1870): W
- Egeria whitii (Lacépède, 1804): E
- Eremiascanus richardsonii (Gray, 1845): U(s), R
- Eulaupis heatwolei Wells & Wellington, 1984: E(ne)
- Eulaupis kosiskuoi (Kinghorn, 1932): E(ne)
- Eulaupis martini (Wells & Wellington, 1985): E(ne)
- Eulaupis murrayi (Bouleguer, 1887): E
- Eulaupis quoyii (Duméril & Bibron, 1839): U(e)
- Eulaupis tenuis (Gray, 1831): U(s), R
- Hemiergis decresiensis (Cuvier, 1829): U(p)
- Lambropilus aniculata Ingram & Rawlinson, 1981: E
- Lampropholis caligula Ingram & Rawlinson, 1981: E(ne), R
- Lampropholis delicata (De Vis, 1888): E
- Lampropholis elongata Greer, 1997: E(ne), R
- Lampropholis guichenoti (Gray, 1839): E
- Lerista bougainvillii (Gray, 1839): W
- Lerista mulleri (Fischer, 1881): W(nw)
- *Lerista punctatovittata* (Günther, 1867): W(sw), R
- Lygusaurus foliolor De Vis, 1884: W
- Menetia greyii Gray, 1845: E(ne), R
- Morethia boulengeri (Ogilby, 1890): W
- Nanoscincus maccoyi (Lucas & Frost, 1894): R
- Ophioscincus truncatus (Peters, 1876): E, R
- Pseudoemoia pagenstecheri (Lindholm, 1901): S
- Saiphos equalis (Gray, 1825): E
- Saproscincus mustelinus (O'Shaughnessy, 1874): E
- Saproscincus rosei Wells & Wellington, 1985: E
- Tiliqua scincoides (White, ex Shaw, 1790): W

Generic representation of 100%. There also is a high representation of Australian typhlopid (50%), scincid (63%) and elapid (85%) genera in New England but lesser generic representation by gekkonids, pygopodids, agamids, boids and colubrids (22-39%) (Table 2). Being inland, New England lacks the predominantly marine families of snakes.
TABLE 1 (Cont.).

SNAKES

FAMILY TYPHLOPIDAE (Blind Snakes or Worm Snakes)
Ramphotyphlops bituberculatus (Peters, 1863): W(sw), R
Ramphotyphlops nigrescens (Gray, 1845): U(e)
Ramphotyphlops proximus (Waite, 1893): W(sw), R
Ramphotyphlops wiedii (Peters, 1867): W

FAMILY BOIDAE (Pythons)
Antaresia maculosa (Peters, 1873): W, R
Morelia spilota (Lacèpede, 1804): U(p)

FAMILY COLUBRIDAE
Boiga irregularis (Merrem, 1802): E, R
Dendrelaphis punctulata (Gray, 1827): E(ne), R

FAMILY ELAPIDAE
Acanthophis antarcticus (Shaw & Nodder, 1802): E, R
Austrelaps ramsayi (Krefft, 1864): E(se)
Cacophis harriettae (Creffi, 1869): E, R
Cacophis krefftii Günther, 1863): E, R
Drysdalia coronoides (Gunther, 1858): U(p)
Furina diadema (Schlegel, 1837): W

**Denisonia devisi** (Waite & Longman, 1920: W

Demansia psammophis (Schlegel, 1837): W
Hemiaspis signata (Jan, 1859): E
Hoplocephalus bitorquatus (Jan, 1859): U(s)
Hoplocephalus stephensii Krefft, 1869: E(ne), R
Notechis scutatus (Peters, 1861): E
Pseudechis guttatus De Vis, 1905: W
Pseudechis porphyriacus (Shaw, 1794): E
Pseudonaja textilis (Duméril, Binbr & Duméril, 1854): W
Rhinoelap察otus nigrescens (Günther, 1862): E
Simoselaps australis (Krefft, 1864): W
Suta dwyeri (Worrell, 1956): U(e)
Suta suta (Peters, 1863): W, R
Tropidechis carinatus (Krefft, 1863): E, R
Vermicella annulata (Gray, 1841): U(e)

DISTRIBUTIONAL PATTERNS

The distributions of all species (Figs 3-108) can be grouped into several general categories. The following interpretations have relied on our database and maps, supplemented by the additional localities on the maps of Swan (1990) and from specimen-based entries in the database of the Atlas of NSW Wildlife (NSW National Parks and Wildlife Service, 2000).

TABLE 2. Representation in New England of the total Australian Squamata. Total genera and species calculated from Cogger (2000); number of genera and species from New England from the present database plus valid additions from Swan (1990).

| Species & genera in New England (New England taxa as % of Australian total) |
|---|---|---|---|---|
| Taxon | Genera | Species | Genera | Species |
| Lizards | | | | |
| Gekkonidae | 18 | 111 | 6(33) | 14(13) |
| Pygopodidae | 8 | 34 | 3(38) | 4(12) |
| Agamidae | 13 | 65 | 5(39) | 10(15) |
| Varanidae | 1 | 26 | 1(100) | 3(12) |
| Scincidae | 38 | 379 | 24(63) | 50(13) |
| Snakes | | | | |
| Typhlopidae | 2 | 40 | 1(50) | 4(10) |
| Booidae | 6 | 15 | 2(33) | 2(13) |
| Acrochordidae | 1 | 2 | 0(0) | 0(0) |
| Colubridae | 9 | 11 | 2(22) | 2(18) |
| Elapidae | 20 | 87 | 17(85) | 22(26) |
| Hydrophiidae | 12 | 31 | 0(0) | 0(0) |
| Laticaudidae | 1 | 2 | 0(0) | 0(0) |
| Total | 129 | 803 | 61(47) | 111(14) |

WIDESPREAD DISTRIBUTIONS. Widespread species usually have broad tolerances and habitat preferences. However, this is not always the case; sometimes widespread distributions may be patchy, reflecting discontinuous habitat within a large area. For example, although Egermia cunninghami is widespread (Fig. 46), it is largely restricted to exfoliating granite outcrops. The occurrences of Physignathus lesueurii and Pseudechis porphyriacus are locally restricted by the distribution of the rivers and other bodies of water with which they are closely associated. In other cases, especially in fossorial or secretive species, patchiness may be more apparent than real; a species like Pygopus lepidopodus may be recorded only sparsely from an area merely because it is difficult to find.

Twenty-two species (20% of the total squamata fauna) were widespread in New England. Of these about equal numbers were evenly widespread in the area (8 species), and widespread but patchily (7 species) or sparsely (7 species) distributed over the region (Table 1).

EASTERN VERSUS WESTERN DISTRIBUTIONS. There are gradients in climate and natural vegetation in New England from east to west; accordingly, 74% of the species have either a predominantly western distribution, or a predominantly eastern one. The Great Dividing Range coincides with the boundary of the geographic range of only a few species (e.g., Gehyra dubia, Eulamprus kosciuskoi) and in some others, distributions have penetrated slightly to the opposite side only in a few small areas (e.g., Oedura lesueurii, Oedura tryoni,
FIG. 3. Amphibolurus burnsi

FIG. 4. Amphibolurus muricatus

FIG. 5. Amphibolurus nobbi

FIG. 6. Physignathus lesueurii

FIG. 7. Pogona barbata

FIG. 8. Pogona vitticeps

FIG. 9. Tympanocryptis lineata

FIG. 10. Tympanocryptis tetraporophora

FIG. 11. Varanus gouldii
FIG. 21. *Oedura monilis*  
FIG. 22. *Oedura robusta*  
FIG. 23. *Oedura tryoni*  
FIG. 24. *Saltuarius swaini*  
FIG. 25. *Saltuarius wyberba*  
FIG. 26. *Underwoodisaurus milii*  
FIG. 27. *Underwoodisaurus sphyurus*  
FIG. 28. *Delma plebeia*  
FIG. 29. *Delma tincta*
FIG. 30. Lialis burtonis
FIG. 31. Pygopus lepidopodus
FIG. 32. Anomalopus leuckartii

FIG. 33. Anomalopus mackayi
FIG. 34. Anomalopus verreauxi
FIG. 35. Bassiana platynota

FIG. 36. Calyptotis ruficauda
FIG. 37. Calyptotis scutirostrum
FIG. 38. Carlia tetradoactyla
FIG. 39. *Carlia vivax*

FIG. 40. *Cautula zia*

FIG. 41. *Coeranoscincus reticulatus*

FIG. 42. *Cryptoblepharus virgatus*

FIG. 43. *Ctenotus robustus*

FIG. 44. *Ctenotus taeniolatus*

FIG. 45. *Cyclodomorphus michaeli*

FIG. 46. *Egernia cunninghami*

FIG. 47. *Egernia frerei*
FIG. 50. *Egernia modesta*

FIG. 49. *Egernia mcpheei*

FIG. 48. *Egernia major*

FIG. 51. *Egernia saxatilis*

FIG. 52. *Egernia striolata*

FIG. 53. *Egernia whitii*

FIG. 54. *Eremiascincus richardsoni*

FIG. 55. *Eulamprus heatwolei*

FIG. 56. *Eulamprus kosciuskoi*
FIG. 57. *Eulamprus martini*

FIG. 58. *Eulamprus murrayi*

FIG. 59. *Eulamprus quoyii*

FIG. 60. *Eulamprus tenuis*

FIG. 61. *Hemiergis decresiensis*

FIG. 62. *Lampropholis amicula*

FIG. 63. *Lampropholis caligula*

FIG. 64. *Lampropholis delicata*

FIG. 65. *Lampropholis elongata*
NEW ENGLAND LIZARDS AND SNAKES

FIG. 66. Lampropholis guichenoti
FIG. 67. Lerista bougainvillii
FIG. 68. Lerista muelleri

FIG. 69. Lygisaurus foliorum
FIG. 70. Menetia greyii
FIG. 71. Morethia boulengeri

FIG. 72. Nannoscincus maccoyi
FIG. 73. Ophioscincus truncatus
FIG. 74. Pseudemoia pagenstecheri
FIG. 75. *Saiphus equalis*

FIG. 76. *Saproscincus mustelina*

FIG. 77. *Saproscincus rosei*

FIG. 78. *Tiliqua scincoides*

FIG. 79. *Ramphotyphlops bituberculatus*

FIG. 80. *Ramphotyphlops nigrescens*

FIG. 81. *Ramphotyphlops proximus*

FIG. 82. *Ramphotyphlops wiedii*

FIG. 83. *Antaresia maculosa*
FIG. 84. *Morelia spilota*

FIG. 85. *Boiga irregularis*

FIG. 86. *Dendrelaphis punctulata*

FIG. 87. *Acanthophis antarcticus*

FIG. 88. *Austrelaps ramsayi*

FIG. 89. *Cacophis harriettae*

FIG. 90. *Cacophis krefftii*

FIG. 91. *Cacophis squamulosus*

FIG. 92. *Demansia psammophis*
FIG. 93. Denisonia devisi
FIG. 94. Drysdalia coronoides
FIG. 95. Furina diadema

FIG. 96. Hemiaspis signata
FIG. 97. Hoplocephalus bitorquatus
FIG. 98. Hoplocephalus stephensii

FIG. 99. Notechis scutatus
FIG. 100. Pseudechis guttatus
FIG. 101. Pseudechis porphyriacus
FIG. 102. *Pseudonaja textilis*

FIG. 103. *Rhinopecephalus nigrescens*

FIG. 104. *Simoselaps australis*

FIG. 105. *Suta dwyeri*

FIG. 106. *Suta suta*

FIG. 107. *Tropidechis carinatus*

FIG. 108. *Vermicella annulata*
Egernia modesta, Hemiaspis signata). However, the topography is not severe on the continental divide and it is unlikely to constitute a physical barrier to dispersal for many species. For a number of species, the boundary of the geographic range lies considerably to one side or the other of the continental divide (e.g., Anomalopus leuckartii, Bassiana platynota, Lampropholis delicata, Lampropholis guichenoti, Pseudechis porphyriacus). In such cases, it is likely that distribution is limited by one or more climatic parameters with an east-west gradient (see below), rather than by the Great Dividing Range itself.

Some of the eastern species certainly can disperse beyond the Great Dividing Range as there are outlier populations on the western edge of the study area at Mt Kaputar, where elevation, rainfall and vegetation parallel those on the eastern side, but differ from those of the western areas surrounding the mountain. Such outliers are: Bassiana platynota, Ctenotus taeniolatus, Egernia cunninghami, Egernia whitti, Eulamprus heatwolei, Hemiergis decresiensis, Lampropholis delicata, Pseudemoia pagenstecheri and Rhinoplocephalus nigrescens. Conversely, a few predominantly western species (e.g., Heteronotia binoei) are found in a few localities in the east.

A number of the species that are predominantly western within the confines of New England are absent or uncommon in eastern New England because of their exclusion from the wetter forests of that region; beyond that gap their ranges do extend eastward, often to the coast. Examples are Oedura robusta, Lygisaurus foliorum, Tiliqua scincoides, Ramphotyphlops wiedii, Demansia psammophis, Furina diadema, Pseudonaja textilis and Simoselaps australis.

There are slightly more species with a predominantly western distribution (40%) than a predominantly eastern one (30%). The difference may be even more disparate than these figures suggest, as there are a number of western species, e.g., Trachydosaurus rugosus, Pseudechis australis, that have been found near, but not inside, the western boundary of New England. With further collecting, or upon completion of some of the surveys still in progress, the ranges of some of these will likely be found to extend into New England.

Infrequently encountered. A salient aspect of the New England reptilian fauna is the large number of species that were recorded from only a small number of localities (‘R’ in Table 1). In many cases, supplementation by the additional localities mapped by Swan (1990) allowed allocation of these species to one of the distributional categories mentioned above. The remaining (4 species) were represented by only one locality in New England and supplementary.
information was not available to aid in interpretation of their local distributional pattern. For example, *Nannoscincus maccovi* (Fig. 72) was found at only one locality, southeast of the center of New England. This is a considerable range extension as formerly it was not known north of Sydney (Swan, 1990). It is likely that the ranges of such species will be extended with further information, or these localities shown to be outliers.

Some of these R species may be rare; in other cases they may be more common than suggested by their frequency in collections because they are secretive and therefore less subject to being found. Gibbons et al. (1997) noted that over a long period of collecting, the known extent of distributions tend to increase remarkably and species' ranges often are much broader than indicated by less intensive collecting.

**RELATION OF DISTRIBUTION TO ENVIRONMENTAL CONDITIONS**

In the following account, the range of conditions under which the various species are found within New England is given. Outside of New England some of these species may extend into areas with environments beyond the limits encountered within the study area. Where correlations are made between distributional patterns and particular levels of environmental features, the relationship is referable only to the New England area, not to the geographic range of a species as a whole.

**ELEVATION.** The lowest elevations (below 400m) are located at the edges of the region in the northwest, southwest and southeast. These slope upward to the New England plateau of 800-1200m in the eastern half of the region with isolated areas up to more than 1400 m, especially near the southern boundary and from the east-central region to the eastern border (Fig. 109).

The frequency of collecting localities had a unimodal distribution skewed toward the middle elevations. The greatest frequency of occurrence was at 100-1100m and the second greatest at 900-1000m. From these values there was a progressive decrease toward the extremes of the range of elevations.

All 26 species for which there were sufficient data for statistical testing of distributions against category of elevation were found at a wide variety of elevations. Of these, seven were distributed randomly with respect to elevation, seven were over-represented at the lower elevations, two at the middle elevations, three at middle to high elevations and seven at the higher elevations (Table 3).

**CLIMATE. Rainfall.** A map of New England with a rough approximation of the isohyets was presented in the first paper of this series (Heatwole & Simpson, 1986). A more detailed map showing the distribution of rainfall was used for the present analyses (Fig. 110). The western and northwestern parts of the region have relatively low mean annual rainfall (mostly 800mm or less) increasing toward the east. The eastern border is especially wet with rainfall >1700mm per annum occurring just to the east and southeast of the designated boundary.

The collecting sites were distributed unimodally with respect to rainfall categories, but skewed toward the lower levels of precipitation. Almost a third of the sites were in areas characterised by 700-800 mm of rain per annum, and the next highest frequency was in the 800-900mm category. All other categories individually contained <13% of the collecting sites.

Of the 14 species for which there were sufficient data for statistical testing, all occurred over most of the spectrum of rainfall values and two species were randomly distributed with
TABLE 3. Distribution of species or reptiles in relation to various environmental parameters. R=random; -- indicates that expectation was lower than 5 in the smallest category and therefore not testable statistically. * 'Other' refers to minor soil or rock types lumped into one category for statistical testing; CP=Chocolate Prairie; RP=Red Podzolic; YS/YP=Yellow Sol/Yellow Pod; YP/GP=Yellow Pod/Gley Pod.

<table>
<thead>
<tr>
<th>Species</th>
<th>Elevation</th>
<th>Rainfall</th>
<th>Coldest Month Minimum Temp</th>
<th>Hottest Month Maximum Temp</th>
<th>Vegetation</th>
<th>Soil Type</th>
<th>Rock Type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Heteronotia binoei</td>
<td>Lower</td>
<td>—</td>
<td>—</td>
<td>26°-32°</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Oedura lesueurii</td>
<td>Middle</td>
<td>Low-Med</td>
<td>-4° to 1°</td>
<td>25°-28°</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Oedura tryoni</td>
<td>Lower</td>
<td>Low-Med</td>
<td>-4° to 1°</td>
<td>26°-32°</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Amphibolurus nobbi</td>
<td>Lower</td>
<td>Low-Med</td>
<td>R</td>
<td>26°-32°</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Amphibolurus muricatus</td>
<td>R</td>
<td>R</td>
<td>-4° to -1°</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Anomalopus leucartii</td>
<td>Lower</td>
<td>Low-Med</td>
<td>R</td>
<td>26°-32°</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Bassiana platynota</td>
<td>Higher</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Calyptotis scutirostrum</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
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<td>Clemotes robustus</td>
<td>Lower</td>
<td>Low-Med</td>
<td>—</td>
<td>26°-32°</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Clemotes laenioliatus</td>
<td>Higher</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Egernia cunninghami</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>Granite</td>
</tr>
<tr>
<td>Egernia striolata</td>
<td>Lower</td>
<td>Low-Med</td>
<td>R</td>
<td>26°-32°</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Egernia whitii</td>
<td>Higher</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Eulamprus murrayi</td>
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<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Eulamprus quoyii</td>
<td>R</td>
<td>Medium-High</td>
<td>0°</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Hemiergis decresiensis</td>
<td>Higher</td>
<td>Low-Med</td>
<td>-4° to -1°</td>
<td>24°</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td>Lamprophis delicata</td>
<td>Middle-High</td>
<td>Medium-High</td>
<td>0° to 6°</td>
<td>21-25°</td>
<td>Woodland; Dry Forest; Wet Forest</td>
<td>RP</td>
<td>R</td>
</tr>
<tr>
<td>Lamprophis guichenoti</td>
<td>Middle-High</td>
<td>Medium-High</td>
<td>0°</td>
<td>21-25°</td>
<td>Wet Forest</td>
<td>RP</td>
<td>R</td>
</tr>
<tr>
<td>Morethia boulengeri</td>
<td>Lower</td>
<td>Low-High</td>
<td>—</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Saiphos equalis</td>
<td>Middle-High</td>
<td>Medium-High</td>
<td>0°</td>
<td>21-25°</td>
<td>Wet Forest</td>
<td>RP</td>
<td>Sedimentary</td>
</tr>
<tr>
<td>Saproscincus roesi</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Ramphotyphlops nigrescens</td>
<td>Higher</td>
<td>—</td>
<td>—</td>
<td>24°-25°</td>
<td>—</td>
<td>—</td>
<td>Basic Igneus; Granite; Other*</td>
</tr>
<tr>
<td>Austrelaps ramsayi</td>
<td>Higher</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Austrelaps superbus</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>Basic Igneus</td>
</tr>
<tr>
<td>Pseudechis porphyriacus</td>
<td>Higher</td>
<td>Low-Med</td>
<td>-1°</td>
<td>21°-24°</td>
<td>—</td>
<td>—</td>
<td>YS/YP; CP; Other*</td>
</tr>
<tr>
<td>Pseudechis textilis</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
<tr>
<td>Suta dwyeri</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
<td>—</td>
<td>—</td>
<td>R</td>
</tr>
</tbody>
</table>

respect to rainfall (Table 3). However, three species were over-represented in areas of low rainfall, five species were found more often than expected on the basis of chance in localities of low to medium rainfall, and four species were proportionately more common in places with medium to high rainfall.

Temperature. Heatwole & Simpson (1986) presented maps (based on Lea et al., 1977 'An Atlas of New England') of the isotherms of the mean daily maxima and minima for the months of July and January, and Heatwole et al. (1995) reproduced one of them (mean daily minimum for July). In general, the central part of the region is the coldest with higher isotherms concentrically arranged toward the periphery.

The present analysis was based on the mean daily minimum of the coldest month (range -4 to
The mean daily minima of the coldest month were unimodally distributed with a peak at and just below freezing, gradually descending toward the higher and lower values. Intervals of mean daily minima of 2°C or above accounted for only slightly more than 9% of the collecting sites and those of 2°C or above for only about 14%.

Of the twelve species for which statistical analysis was feasible, three showed random distribution with regard to levels of mean daily minimum temperature of the coldest month (Table 3). The remainder, while found over most of the spectrum of minimum temperatures, statistically favoured certain levels. Four species tended to occur more often than expected in the coldest localities, four at intermediate localities (near zero), and one was enigmatic, being found more often than expected by chance over a wide range of the higher temperatures.

The mean daily maximum temperature of the hottest month showed a bimodal frequency distribution with one peak at 24°C (20.6% of the collecting sites) and 25°C (21.4%) and the other at 28°C (12.1%); all other temperature intervals individually accounted for <10% of the sites.

Of the 20 species for which statistical testing could be conducted, seven were shown to be distributed at random with respect to mean daily maximum temperature for the hottest month (Table 3). Four species were over-represented in the thermal categories in the range of 21°C-24°C or 21°C-25°C, two in the ranges of 24°C or 24°C-25°C, and seven in various ranges of categories from 25°C and higher.

VEGETATION. The New England area is devoted to the pastoral industry and consequently is highly modified by human activity. Accordingly, many of the collecting sites occurred on cleared land (45%), with disturbed remnants accounting for an additional 11% of the localities. The forest types containing the greatest frequency of occurrence of collecting sites were Dry Forest Complex (19%) and Dry Open Forest (15%); all other vegetation types individually contained 11% of the sites (Fig. 113).

Each of the previous papers in this series has used a different classification of vegetation or land-use. The present analysis is based on a modification of the classification of vegetation systems for northeastern New South Wales (NSW National Parks and Wildlife Service, 1994).

Only three species could be tested because of the small areas occupied by wet forests and the statistical limitations this imposed. Saiphos equalis and Lampropholis guichenoti were found in wet forest significantly more often than expected at random, whereas Lampropholis delicata was over-represented in woodlands and in both dry and wet forests (Table 3).

SOIL TYPE. The soil types (Fig. 114) accounting for the greatest number of collecting localities were Yellow Pod/Grey Pod (24% of the sites), Red Podzolic (21%) and Yellow Sol/Yellow Pod (19%); the other 15 soil types each accounted for <10% of the collecting localities and collectively for 36%.

Eleven species were tested against the distribution of soil types. Of these, two were distributed randomly with respect to soil type (Table 3), three were found oftener than expected by chance on red podzolic soils, and five were over-represented on more than one soil type, but always involving yellow sol/yellow pod and/or yellow pod/gley pod soils in combination with others.
ROCK TYPE. The two most abundant rock types characterising collecting sites were sedimentary rocks with low quartz (36% of the collecting sites) and granite (23%); all other rock types accounted for 13% or less of the collecting localities (Fig. 115).

Twenty-three species allowed for statistical testing of distribution against the various rock types, of which 12 were randomly distributed, five were over-represented on granite, four on basic igneous, and two on sedimentary rocks (Table 3).

Only three species could be tested against all environmental characteristics (Table 3). Lampropholis delicata showed random distribution only with respect to parent rock type and consequently all other characteristics may have affected its distributional patterns. It is over-represented at middle to high elevations, in woodlands and forests on red podzolic soils where there is medium to high rainfall and where mean minimum temperature of the coldest month is zero°C or above and mean maximum temperature of the hottest month is in the range of 21°-25°C. L. delicata does occur under other conditions, but is under-represented there and thus it would appear that this suite of environmental conditions defines the optimum habitat of this species.

Lampropholis guichenoti had an almost identical distribution to L. delicata. It differed only by being over-represented in a narrower range of minimum temperatures of the coldest month (0°C only, rather than the larger range 0°-6°C), in only wet forest rather than multiple kinds of forest, and by being randomly distributed relative to soil type. Despite their great similarity, and their great overlap in distribution, these two species seem to have minor differences in the biographical details.

Saiphos equalis is distributed very similarly to L. guichenoti except that it is over-represented on sedimentary rocks instead of being randomly distributed with respect to rock type.

Eight species could be tested against all environmental characteristics except vegetation (the characteristic allowing for the testing of the fewest number of species) (Table 3).

The most clear-cut result was for Egernia cunninghami, which was distributed randomly with respect to all environmental characteristics measured except it was over-represented on granite. This species inhabits crevices in exfoliating...
rocks throughout its range (Cogger, 2000); granite is especially prone to such structure. It is not surprising that the distribution of *E. cunninghami* is strongly related to the occurrence of this primary feature of its habitat.

Similarly, *Amphibolurus muricatus* that showed random distribution with respect to all environmental parameters tested except for mean minimum of the coldest month; this species was over-represented in the coldest part of the area (Table 3). The remaining six species in this category departed from randomness in respect to a number of parameters and distributional patterns may be influenced in more complex ways than for *A. muricatus* and *E. cunninghami*.

For the remaining species tests there were three or more environmental parameters for which tests could not be conducted and consequently optimal habitats are defined less completely. *Heteronotia binoei* and *Egernia striolata* are distributed randomly with respect to rock type, *Suta dwyeri* and *Pseudonaja textilis* to elevation, maximum temperatures and rock type, *Saproscincus rosei* to elevation and rock type, *Calyptotis scutirostrum* to elevation, *Ctenotus taeniolatus* to maximum temperatures, and *Morethia boulengeri* to maximum temperatures and rock type. Some of the species with a limited number of available tests were over-represented on some categories. *Heteronotia binoei* was over-represented at lower elevations and high maximum temperatures, *Bassiana platynota* at high elevations, *Ctenotus robustus* at low rainfall (see above), low elevation, and high maximum temperatures, *Ctenotus taeniolatus* to high elevations, *Egernia striolata* at low elevations, *Egernia whitii* at high elevations, *Eulamprus murrayi* at middle elevations, *Morethia boulengeri* at low elevations and low to medium rainfall, *Ramphotyphlops nigrescens* at high elevations and maximum temperatures in midrange, and *Austrelaps ramsayi* at high elevations (Table 3).

Various of the environmental attributes of the region are correlated with each other (e.g., temperature, elevation, and rainfall) and hence...

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**FIG. 113.** Vegetation systems of the study area. Derived from broad vegetation boundaries mapped on 1:100k Landsat imagery. Mapping undertaken by NPWS in 1991.

**FIG. 114.** Distribution of the various soil types in the study area. From the Atlas of New England (Lea et al., 1997), digitised and executed using Environmental Research Mapping Scheme (Ferrier, 1989), NPWS, NSW, Armidale office.
the precise factor or combination of factors that proximally affects distribution cannot be identified individually from the present data. However, assembling the suite of environmental levels at which a species shows over-representation, permits definition of its optimal habitat, and allows construction of testable hypotheses about proximal factors affecting distributions. Detection of features with which a species is randomly distributed is perhaps of even more importance as it identifies environmental parameters that are unlikely to be affecting a species distribution, at least within the range of values encountered in New England.

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LITERATURE CITED


