

no sensory transfer and thus, only the activated memory referents were initially available. On such trials, recognition occurred in reverse: The inferential process appeared to reflect a search through an already activated semantic field for the identity of the original stimulus (14). When the callosum had been completely sectioned, neither sensory nor higher-order information was available to the expressive language system after stimulation of the right hemisphere.

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5. Using the estimating procedure of C. L. Oon [Am. J. Roentgenol. **92**, 1242 (1964)], D. H. W. sectioned approximately the posterior 3 to 4 cm of the callosum in the first operation. For a description of the microsurgical procedure, see D. H. Wilson, A. Reeves, and M. S. Gazzaniga [*Neurology* **28**, 649 (1978)].
6. For visual testing we used standard tachistoscopic techniques to present stimuli briefly (generally for 150 msec), thus ensuring lateralization to a single hemisphere via its contralateral visual field. Auditory testing consisted of a dichotic speech sound identification test, and tactile tests required manipulation outside the field of vision [M. S. Gazzaniga et al. in (3); S. P. Springer, J. J. Sidtis, D. H. Wilson, M. S. Gazzaniga, *Neuropsychologia* **16**, 305 (1978)].
7. Preoperative and postoperative accuracy scores (percentages) on left-sensory-field naming tests are as follows: visual words, 63, 13; tactile objects, 100, 20; and dichotic consonant-vowel syllables, 67, 23. None of the postoperative scores differ from chance.
8. Preoperative and postoperative accuracy scores on right-sensory-field naming tests are as follows: visual words, 93, 91; tactile objects, 100, 90; and dichotic syllables, 77, 100.
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11. Although the data in Table 1 represent performance on repeated administrations of the same picture and word tests, the improvement in performance based on the inference strategy was evident with novel stimuli as well. For example, in the tenth interoperative week, left-visual-field naming of novel words occurred on 71 percent of the trials, whereas right-visual-field performance was at 92 percent.
12. The specificity of the higher-order information available from the right hemisphere suggests that deep dyslexia may not represent right-hemisphere reading.
13. While the transfer of higher-order information may have occurred in both directions, it was not feasible to evaluate transfer from left to right hemispheres (9).
14. Retrieval from memory has been characterized as a spreading activation process [A. M. Collins and E. F. Loftus, *Psychol. Rev.* **82**, 407 (1975)] in which information adjoining the initial referent in memory shares its activation. In somewhat different but compatible terms, the activated field upon which the inference is based can be seen as a memory description constructed by the right hemisphere but evaluated by the left hemisphere [D. A. Norman and D. G. Bobrow, *Cognit. Psychol.* **11**, 107 (1979)].
15. Aided by PHS grant 2 R01 NS15053-02, the Alfred P. Sloan Foundation, the McKnight Foundation, and RR001-02 to Rockefeller University Hospital.

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## Hinged Teeth in Snakes: An Adaptation for Swallowing Hard-Bodied Prey

**Abstract.** Six genera of snakes, representing at least three lineages, possess teeth that fold backward against the jaws rather than being firmly ankylosed. This condition, effected by a connective tissue hinge at the base of each tooth, is associated with suites of cephalic modifications that enable the snakes to grasp and to swallow hard-bodied prey.

The teeth of most snakes are sharp, recurved, and firmly ankylosed to the jaws. Such teeth are ideal for piercing and grasping, but are ill-suited for dealing with hard-bodied prey. Thus, durophagic adaptations (that is, those related to feeding on hard-bodied prey) in snakes have been thought to be limited to reduction of tooth size and number [in the egg-eaters *Dasyptis* and *Elachistodon* (1)] and to modifications facilitating the extraction of soft parts from mollusk shells [in dipsadine and pareine snakes (2)]. I report here a previously unrecognized durophagic adaptation in snakes: hinged teeth (3). Although viperid snakes have fangs capable of considerable movement, this action results from motion between cranial bones, especially the maxillae (to which the fangs are affixed) and the prefrontals. The viperid system is therefore simply an extension of the advanced cranial kinesis typical of snakes. In sharp contrast, six genera have teeth that are attached to the dentigerous bones by flexible connective tissue fibers (4, 5). Typically these teeth are small, numerous, distally flattened, and extremely smooth on their leading surfaces. Although hinged teeth are known in a variety of fishes (6) and lissamphibians [in which the tooth itself is divided into an ankylosed pedicel and a crown which may be movable (7)], hinged teeth have not been reported in amniote vertebrates.

Other changes have accompanied the development of hinged teeth in snakes. Differences in cephalic structure correspond to distinctive tooth morphologies

and permit the recognition of three groups of hinged-toothed snakes. Group 1 includes only the primitive Indomalaysian genus *Xenopeltis*. Group 2 contains three genera of colubrid snakes: the Malagasian *Liophidium*, the northern neotropical *Scaphiodontophis*, and the Indomalaysian *Sibynophis*. These three genera have frequently been united as the subfamily Sibynophiinae; however, their structural similarities pertain largely to the feeding apparatus and may have been derived in parallel (8). Group 3 includes the related African colubrids *Lycophidion* and *Mehelya*.

In group 1, the base of each tooth is expanded and enveloped in a connective tissue sheath. The hinge fibers run from the distolingual quadrant of that sheath to the adjacent bone (Fig. 1, B and C). Opposite the hinge, the bone slopes to form a pedicel. The teeth of small and moderate-sized ( $\leq$  approximately 700 mm, snout-vent length) *Xenopeltis* are distinctly bicuspid (Fig. 1A). The leading surface of each tooth is broad, almost flat, and curved at its tip. Distal to that surface and slightly offset is a pointed cusp. The flat surface is extremely smooth, showing only a fine vermicular ornamentation at approximately  $\times 10,000$  magnification. The teeth of larger individuals are unicuspid, sharp, and strongly recurved. The teeth are numerous (approximately 40 on each maxilla), and almost all tooth positions are occupied simultaneously, indicating an abandonment of the alternate tooth replacement scheme characteristic of other snakes (9).

Some variation obtains in group 2, but a basic pattern is shared. In advanced members of this group (*Scaphiodontophis*, *Sibynophis*, *Liophidium rhodogaster*), the teeth are small and numerous (more than 50 maxillary teeth in some species) (Fig. 1D). The teeth can easily be manipulated into the folded position by pressing against the leading surface. The posteriormost teeth of *L. rhodogaster* are larger than the rest and less effectively hinged. The posteriormost maxillary tooth of *Scaphiodontophis* and *Sibynophis* is also different from the more anterior ones. This suggests an origin of these genera from snakes with enlarged, and possibly grooved, rear teeth. The teeth of *Sibynophis* are scarcely enlarged at the base, but those of *Liophidium* and *Scaphio-*

*dontophis* are noticeably so. Those of *Scaphiodontophis* are also flared basally (Fig. 1G).

The hinge of *Liophidium* consists of short connective tissue fibers running from the distolingual base of the tooth to the adjacent bone (Fig. 1I). A well-developed cone of tissue projects into the concave tooth base, and provides a fibrous connection to the distolabial region from within. In *Sibynophis* the fibers of the hinge, located as in *Liophidium*, have a less direct orientation, traversing horizontally to insert on the bone. The central cone is poorly developed, and bony pedicels are only slightly more prominent than in *Liophidium*. The hinge of *Scaphiodontophis* emerges from a low connective tissue sheath as a network of fibers in the distolabial region. There is a

well-developed basal cone, which sends abundant fibers to the region of the hinge. In serial sections, the hinge of *Scaphiodontophis* appears as a crescent of tissue around the mesial base of the tooth and contiguous with the fibers of the central cone (Fig. 1H). Bony pedicels are better developed in this genus than in the preceding two.

The tips of the teeth of *Sibynophis* are rounded in profile and noticeably flattened distally. Those of *Liophidium rhodogaster* and *Scaphiodontophis* show both distal expansion and compression, resulting in strongly spatulate teeth (Fig. 1, G and I). The mesiolabial surfaces of the teeth of the three genera exhibit virtually no relief at  $\times 10,000$  (Fig. 1F), although the distolingual surface is highly sculptured (Fig. 1E). This difference is

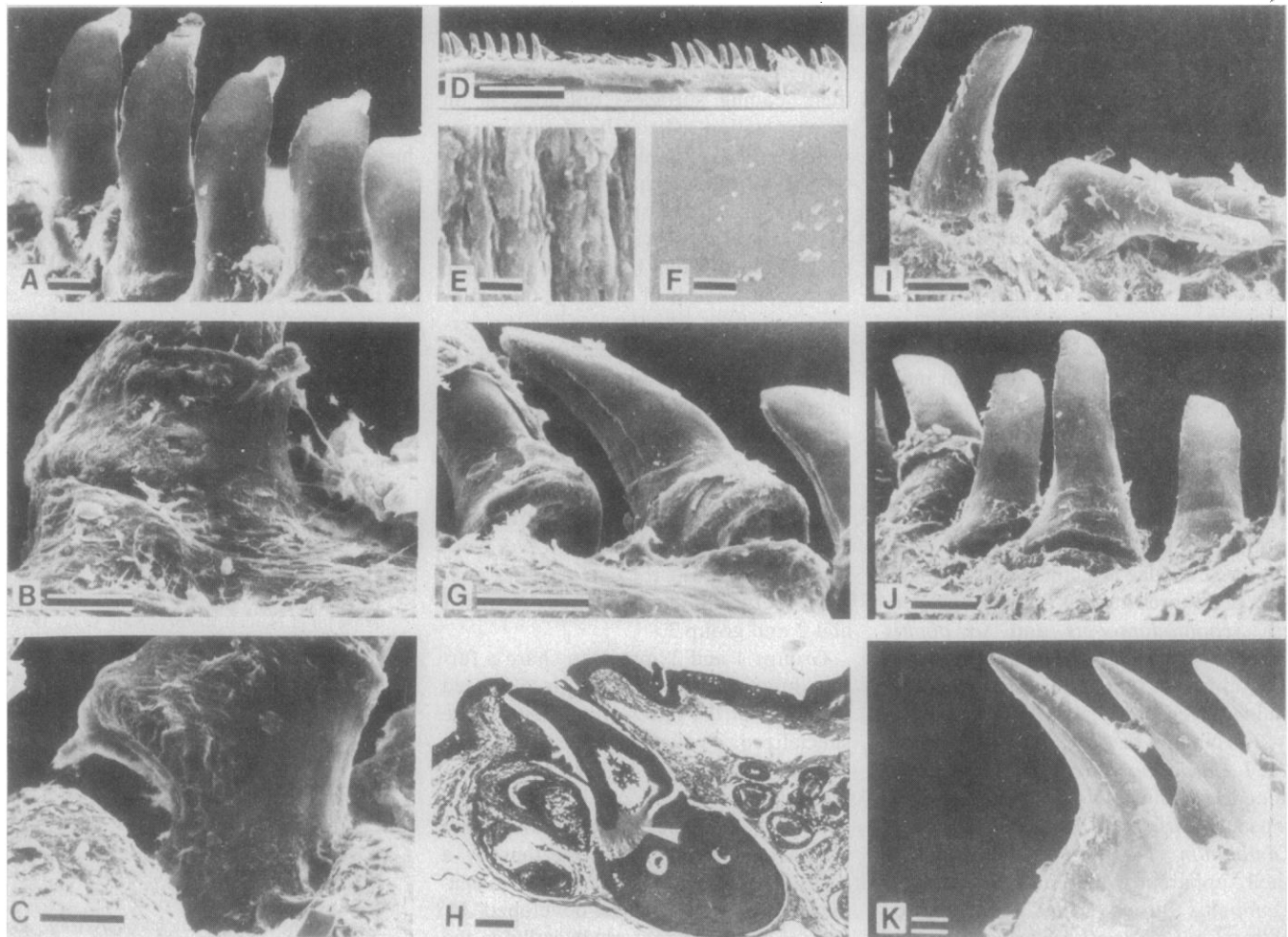


Fig. 1. Scanning electron micrographs (A to G and I to K) and light photomicrograph (H) of maxillae and maxillary teeth of snakes, illustrated in inverted position. (A to C) *Xenopeltis unicolor* (left maxilla): (A) occlusomesiolabial view of bicuspid teeth with broad leading surface; (B) lingual view of base of tooth in erect position; and (C) lingual view of base of tooth in partly inclined position. (D to G) *Scaphiodontophis annulatus* (left maxilla): (D) labial view of tooth row (central teeth were held in folded position during critical point drying); (E) detail of distolingual surface of tooth, demonstrating considerable relief; (F) detail of mesiolabial surface of tooth, demonstrating virtual absence of relief; and (G) occlusolabial view of folded tooth, showing spatulate tip and smooth leading surface. (H) *Scaphiodontophis venustissimus* (right maxilla); cross section through tooth and surrounding tissue [arrow indicates hinge fibers, which attach tooth (above) to maxilla (below)], stained with Mayer's alum hematoxylin and counterstained with safranin O. (I) *Liophidium rhodogaster* (left maxilla); lingual view of erect tooth (left) and reclined tooth (right). (J and K) *Lycophidion capense* (left maxilla); (J) mesiolabial view of small, hinged postdiastemal tooth, showing absence of ankylosis, flattened tip, and smooth leading surface; and (K) labial view of large, ankylosed prediastemal tooth, showing relatively conical shape. Scale: (A to C and G to K) 0.1 mm; (D) 1.0 mm; and (E and F) 0.001 mm.

attributable to a smooth mesiolabial coating (probably enamel), whose edges are clearly visible (Fig. 1G). The few empty sockets in all genera indicate abandonment or modification of alternate tooth replacement.

Within *Liophidium*, considerable variation in the aforementioned features exists. In species such as *L. vaillanti*, the teeth are less compressed, kinetic, and numerous than those of *L. rhodogaster*, which seems to be the most derived species of its genus.

Members of group 3 exhibit two distinct maxillary tooth morphologies. A short distance from the anterior end of the bone are two enlarged, pointed, almost conical teeth (Fig. 1K), which are firmly ankylosed to the bone except during replacement. Anterior to these, the teeth gradually decrease in length, and are compressed at the tips. Posterior to the enlarged teeth is a diastema, followed by a longer series of short, flattened teeth (Fig. 1J). Both the anterior and posterior series are attached to the bone by poorly developed hinges consisting of a network of connective tissue fibers in the distolabial quadrant of the tooth base, and rest on poorly defined pedicels. Each tooth, including those that are ankylosed, is smooth on its mesiolabial surface and rough on its distolingual one. Alternate tooth replacement seems not to have been fully superseded in group 3 snakes, although most teeth are simultaneously attached. The tenuous attachment of several teeth suggests incomplete development of their hinges.

Recorded dietary habits of hinged-toothed snakes reveal that lizards of the family Scincidae are consumed by members of all three groups. The group 2 genera *Scaphiodontophis* and *Sibynophis* seem to be virtually restricted to such a diet, although other lizard and snake remains have been reported (10). Similarly, specimens of *Liophidium rhodogaster*, *L. torquatus*, and *L. trilineatus* contained remains of scincid and gerrhosaurid lizards. A single specimen of *Liophidium vaillanti* contained an eggshell, apparently that of a snake (11). *Xenopeltis* (group 1) has been credited with taking a variety of prey, including frogs, various lizards, snakes, birds, and rodents (12), but one specimen reportedly contained four skinks, belonging to three genera, in addition to a young snake (13). Of group 3, *Lycophidion* has been reported to feed predominantly on skinks, although other lizards (including the osteoderm-bearing gerrhosaurids), snakes, and mice are also eaten. Skinks

are also included in the diet of *Mehelya*, although other lizards (including gerrhosaurids and agamids), snakes, anurans, and occasional mammals also have been reported taken. *Mehelya nyassae* is especially credited with a skink diet (14). Thus, although hinged-toothed snakes take a diversity of prey, all genera are known to eat skinks, some almost exclusively. Significantly, that is especially true of genera in group 2, which includes species with the most advanced hinged-tooth mechanism.

Scincid lizards are hard-bodied, relatively nondeformable prey. They are covered with stiff, strongly imbricate, cycloid scales, each of which is underlain by an osteoderm. Such an armor poses the danger of breakage to long, sharp, firmly ankylosed teeth. I propose that the genera under consideration developed hinged teeth as an alternative mechanism to accommodate hard-bodied prey, primarily scincid lizards. Such teeth fold when forces are applied to their leading surfaces, but lock in an erect position when the forces come from behind, as would occur during the retraction movements of ingestion or when a prey item struggles to escape. The compressed tips common to many of the species would then slide between overlapping scales of the prey, thus gaining a purchase without piercing the dermal armor. The relatively cylindrical shape of a skink provides the teeth with a long line of contact. The long tooth rows characteristic of these snakes thus constitute a gliding surface over which prey may be drawn, as well as a ratchet mechanism for guarding against its escape. That basic mechanism, however, appears to constitute the extent of the similarity between the combined groups 1 and 2 and group 3.

Groups 1 and 2 appear to share a further functional strategy, with advanced members of the latter group being more specialized. Typically, the dentary bone of each mandible is highly mobile relative to the strongly curved compound bone, although the paired dentaries are bound inelastically to each other by a cartilaginous plate (group 1) or a ligament (group 2). A well-developed *M. levator anguli oris* inserts broadly on the free posterior end of the dentary, perhaps serving to draw the bone around the prey. The bones of the palatomaxillary arch are dorsoventrally flattened (group 1) or slender (derived species of group 2), and may be sufficiently flexible to absorb forces not countered by the dental hinges. These distinctive features suggest that snakes of groups 1 and 2 have

modified the unilateral feeding mode of most snakes to provide greater bilateral mandibular motion, while maximizing the contact between the tooth rows and the prey.

Snakes in group 3 follow a different strategy. The prefrontal bone articulates parasagittally with the braincase, allowing the strongly arched maxilla to function as a rocker arm. Thus, during palatomaxillary retraction the front of the maxilla could be lowered to engage the large, ankylosed teeth which presumably pierce the prey's armor and may conduct the secretion of Duvernoy's glands (15). Jaw protraction would elevate the enlarged teeth out of contact with the prey and engage the long posterior row of hinged teeth.

These comments regarding the hypothesized function of the feeding apparatus are inferential and can be tested conclusively only by observation of feeding sequences in living specimens. Regardless of the precise cranial mechanics, however, the development of hinged teeth in at least three, and perhaps five, independent lineages of snakes is an unusual and dramatic adaptation for the oral processing of hard-bodied prey.

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3. S. C. Sarker [*Proc. Zool. Soc. London* 1923, 297 (1923)] described "hinged teeth" in several genera of colubrid snakes. As A. M. Taub [*Bull. Am. Mus. Nat. Hist.* 138, 17 (1967)] pointed out, however, Sarker's descriptions and figures refer to the replacement teeth typical of most snakes. Every other tooth in the genera he described was ankylosed. In contrast, none, or at most one alternately replacing pair, of teeth on any single bone are ever ankylosed in the genera described in this report.
4. Descriptions are based on maxillary teeth, and mention of labial and lingual surfaces corresponds to those surfaces on maxillary teeth. "Mesial" and "distal" generally correspond to anterior and posterior, respectively [see figure 1 in (9)]. Maxillae from preserved specimens were excised for scanning electron microscopy; soft tissue and replacement teeth were removed with forceps, cleaned ultrasonically, and transferred gradually to amyl acetate for critical point drying with carbon dioxide. No chemical solvents were used for cleaning. A section of each tooth row was wrapped in the folded position during drying. Specimens were coated with gold-palladium over carbon, examined under a Cambridge Mark IIA Stereoscan, and photo-

graphed on Kodak Graphic Arts film (No. 4127). For serial sections, a 3-mm length of maxilla and surrounding tissue was excised from a preserved specimen, embedded in Paraplast under vacuum, sectioned at 4  $\mu$ m, and treated with a variety of stains.

Specimens examined: Scanning electron microscopy: *Xenopeltis unicolor*, USNM (National Museum of Natural History) 163969; *Liophidium rhodogaster*, USNM 149835; *Scaphiodontophis annulatus* (= *zeteki*), KU (University of Kansas Museum of Natural History) 62125; *Sibynophis chinensis*, USNM 35521; *Lycophidion capense*, USNM 162450; and *Mehelya poensis*, USNM 199297. Histology: *Scaphiodontophis venustissimus*, KU 125493.

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Taxonomic treatment of group 2 snakes follows that of E. C. Morgan, thesis, University of Southwestern Louisiana, Lafayette (1973).

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Food records for these genera are reviewed by A. E. Leviton and H. E. Munsterman [*Occas. Pap. Nat. Hist. Mus. Stanford Univ.* 4, 7 (1956)] and by E. C. Morgan (8, pp. 182-183). The food of *Scaphiodontophis* is also discussed by M. Alvarez del Toro [*Los Reptiles de Chiapas* (Instituto de Historia Natural del Estado [Chiapas], Tuxtla Gutiérrez, ed. 2, 1972), pp. 78 and 112].

Personal observation, based on intestinal contents of the following specimens: *Liophidium rhodogaster*, USNM 149835; *L. torquatus*, AMNH (American Museum of Natural History) 24802, CAS (California Academy of Sciences) 123194, USNM 149249; *L. trilineatus*, AMNH 60672; and *L. vaillanti*, USNM 150599. As intestinal contents, the sample may be biased in favor of relatively durable remains, such as scales and osteoderms. Although a greater variety of prey thus is not precluded, the inclusion of hard-bodied lizards in the diet of *Liophidium* is nevertheless established.

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E. Kochva and M. Wollberg [*Zool. J. Linn. Soc.* 49, 219 (1970)] report a muscularized Duvernoy's gland in *Mehelya poensis* but no Duvernoy's gland whatever in *Lycophidion capense*. Gross and histological examination confirmed their observations on *M. poensis* (USNM 167075 and 199297) but also indicated a non-muscularized serous gland in *L. capense* (USNM 142081 and 162450). In both species the duct of Duvernoy's gland appears to empty in the region of the enlarged maxillary teeth.

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## Aerial Spraying of 2,4,5-T and Human Birth Malformations: An Epidemiological Investigation

**Abstract.** An investigation of the rate of birth malformations in the Northland region of New Zealand provides no evidence to associate spraying of 2,4,5-trichlorophenoxyacetic acid with the occurrence of any malformation of the central nervous system, including spina bifida. A statistically significant association between spray and malformation is found in the case of talipes. Whether this association indicates a causal relation remains to be established.

Considerable interest has focused on the possible effects of the herbicide 2,4,5-trichlorophenoxyacetic acid (2,4,5-T) and its contaminant 2,3,7,8-tetrachlorodibenzo-*p*-dioxin (TCDD) on human health and environment (1). In this investigation, hospital records were used to identify the rates of occurrence of all diagnosed malformations, including stillbirths and neonatal deaths, but excluding miscarriages at less than 28 weeks fetal age, in specific areas of Northland, New Zealand, for each month over the period 1960 to 1977. These rates were compared with the densities of monthly aerial 2,4,5-T spray application in the same area during the same period. Seven mutually exclusive areas were defined, each centered on one of the region's maternity hospitals: Dargaville, Rawene, Kaitaia, Whangarei, Kawakawa, Kaikohe, and Kaeo.

During the study period, 37,751 babies

were born in Northland hospitals; 436 of these were stillborn, 264 died shortly after birth, and 510 had diagnosed malformations (2). It is estimated that in Northland, as in the rest of New Zealand, well over 99 percent of all births occur in hospitals.

Aerial spraying of 2,4,5-T is carried out in Northland by a number of companies, and from the records each made available, it was possible to identify the site of each spray job and the quantity and date of 2,4,5-T application (3). As no aerial spraying took place in Northland in the first half of the 1960's, calendar years 1959 to 1965 were chosen as representative of those without environmental 2,4,5-T, and 1972 to 1976 as representative years with 2,4,5-T spraying. Within that period there was considerable variation in the quantity of 2,4,5-T applied in each year, in each month, and in each of the seven areas.

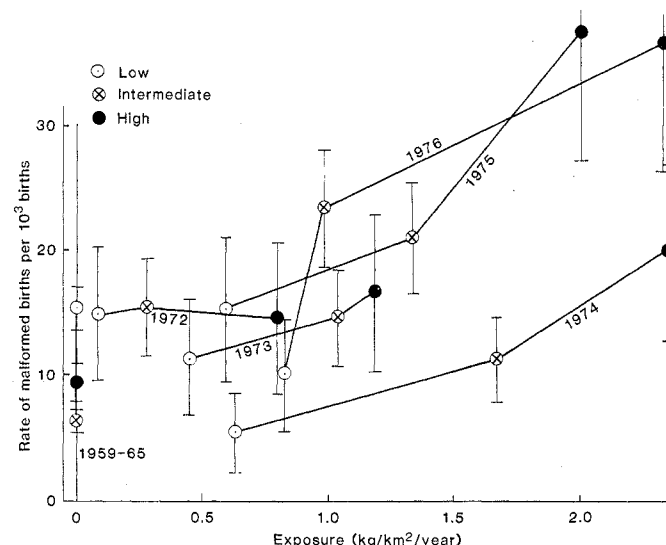


Fig. 1. Distribution of birth malformations during years of no spraying (1959 to 1965), which are treated as 1 year, and from 1972 through 1976. Areas of low, intermediate, and high averaged annual spray density correspond to the various hospital areas: low includes Dargaville, Rawene, and Kaitaia; intermediate is Whangarei; and high includes Kawakawa, Kaikohe, and Kaeo. Poisson error bars are shown: decay hypothesis,  $f = 1.00$ .