

## Identification of *Phytophthora* spp. known to Attack Conifers in the Pacific Northwest

### Abstract

Fungi belonging to the genus *Phytophthora* are some of the most destructive plant pathogens worldwide. Unlike most plant pathogens, members of this genus produce swimming zoospores that follow a gradient of root exudates to host tissue. In the Northwest, *Phytophthora* diseases are most damaging on crops in poorly drained or irrigated soils. Species are difficult to isolate and even more difficult to identify. Of the more than 50 *Phytophthora* species described worldwide, nine are associated with serious diseases on conifers grown in the Pacific Northwest. Physiological and morphological characteristics of these species are described which are particularly useful when identifying Pacific Northwest isolates. Methods for observing the fungi are provided along with a key to simplify species identification. The geographical range within the region and conifer hosts attacked are identified.

### Introduction

*Phytophthora* spp. cause serious diseases in Pacific Northwest conifers. *Phytophthora lateralis* Tuck. & Milb. kills indigenous Port-Orford-cedar (*Chamaecyparis lawsoniana*) [A. Murr.] Parl. in the forests of southwestern Oregon and northern California (Roth *et al.* 1957, Zobel *et al.* 1985, Kliejunas and Adams 1981) and, along with *P. cinnamomi* Rands., is a fatal root pathogen of Port-Orford-cedar in ornamental plantings (Torgeson *et al.* 1954). Species that cause damage to a wide range of conifer seedlings in Oregon, Washington, and British Columbia nurseries include *P. cryptogea* Peth. and Lef., *P. cactorum* (Leb. and Cohn.) Schr., *P. drechsleri* Tucker, two distinguishable groups of *P. megasperma* Drech. emend Hamm & Hansen, *P. pseudotsugae* Hamm & Hansen, and *P. cinnamomi* Rands (Hamm *et al.* 1985; Pratt *et al.* 1976, Hansen *et al.* 1980, Hamm and Hansen 1982a, 1982b, 1983; Kanaskie, pers. comm.). Recently *P. cambivora* was associated with root rot and stem cankers on Noble fir grown for Christmas trees (P. B. Hamm and G. A. Chastagner, unpublished data).

In the past, *Phytophthora* spp. may have been overlooked as a cause of tree mortality because of difficulties in isolation, recognition, and identification of the pathogen. Recent advances in chemical control (Hamm *et al.* 1984) and information on the host preferences of these fungi can be useful in disease management, but only after the pathogens are properly identified. Because more than 50 species of *Phytophthora* are

described worldwide (Waterhouse and Blackwell 1954; Waterhouse 1963, 1970; Newhook *et al.* 1978) a simplified key is needed for identifying those species that are specifically associated with Pacific Northwest conifers. By limiting the number of *Phytophthora* species included, a regional identification key (such as that published for the British Isles by Waterhouse and Blackwell [1954]) can use characteristics (usually physiological) specific to local isolates which could not be used in a worldwide key. This paper presents such a regional key for identifying *Phytophthora* species known to attack Pacific Northwest conifers.

### Characteristics of *Phytophthora*

#### Oogonia and oospores

*Phytophthora* has a diploid life cycle. A single, spherical oospore is formed within an oogonium following attachment (fertilization) by a one or two-celled antheridium. The presence of oospores, location of antheridial attachment, the sizes of these structures, and whether the oogonial wall is smooth or ornamented are important features in distinguishing *Phytophthora* spp. Oospores may be formed by a single isolate (homothallic species) or only by mating two sexually different isolates (heterothallic species). Antheridia attach either around the oogonial stalk (amphigynous) or elsewhere on the oogonium (paragynous), sometimes adjacent to the stalk (Figure 1). Oospores are distinguished from similarly shaped chlamydospores by the presence of two walls—the external oogonial wall and an internal, often thicker wall around the oospore itself—and by the presence of antheridia.

Most homothallic species from Pacific Northwest conifers form oogonia on clarified V-8 agar after 1-3 weeks in the dark at room temperature. To prepare clarified V-8 agar: add 200 ml of V-8® juice to 1.5 g calcium carbonate, heat for 5 minutes in an autoclave, and then centrifuge for

15 minutes at 2,000 RPM. To each 200 ml of supernatant add 800 ml distilled water and 15 g of agar, then autoclave (Pratt and Mitchell 1973). If oogonia have not formed within 4 weeks, repeat the procedure with fresh agar. Repeated failure suggests a heterothallic species, which should be paired with known isolates of both mating types to confirm heterothallism.

#### Chlamydo spores

Chlamydo spores are spherical, relatively thick-walled, single-celled spores, formed by some species of *Phytophthora*, and presumably function as resting structures. They develop in clarified V-8 agar and can be either intercalary or terminal (Figure 1). They are delimited from subtending hyphae by septa, which also distinguish them from hyphal swellings which are not walled off. As mentioned previously, chlamydo spores differ from oogonia by their lack of a double wall or of an antheridium.

#### Hyphal-swellings

Spherical, ellipsoid or irregular swellings may form terminally or intercalary on vegetative hyphae. In appearance hyphal swellings differ from oogonia by their lack of double walls and antheridia, and from chlamydo spores by lack of septations.

#### Sporangia

The asexual zoospores of *Phytophthora* are produced within sporangia when colonies are in water or saturated soil. Sporangia generally are spherical, ovoid, obpyriform or ellipsoid in shape and are either papillate (i.e., having a terminal protrusion, Figure 1c) or non-papillate (Figure 1d). Sporangial shape and size vary with age and growth conditions so they should be observed when first formed. Zoospores of *Phytophthora* differentiate within the sporangia and are released fully formed directly into water. In contrast, zoospores of *Pythium*, a similar and closely related genus, do not form until the undifferentiated sporangial protoplasm has extruded into a vesicle attached to the sporangium (Figure 1H).

Usually sporangia are produced on colonies grown in pea broth (150 g of split peas in 1 L of distilled water, heated in an autoclave for three minutes, filtered through double cheesecloth,

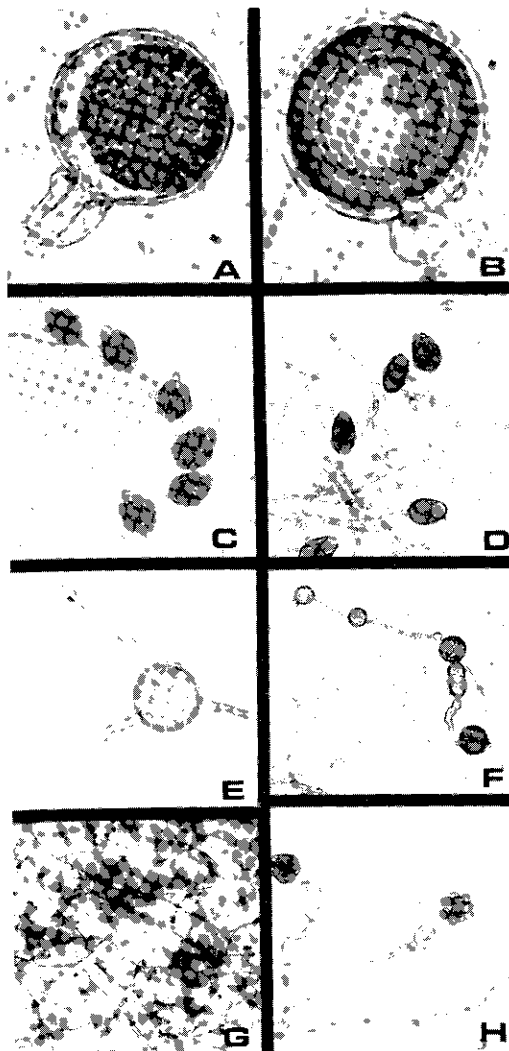


Figure 1. Oogonia, sporangia and chlamydo spores characteristic of *Phytophthora*. (A) Oogonia containing oospores with amphigynous and (B) paragynous antheridia. (C) Sympodially born papillate sporangium. (D) Ovoid and ellipsoid sporangia. (E) Hyphal swelling. (F) Terminal and intercalary chlamydo spores on one hypha. (G) Mycelia characteristic of *P. cinnamomi*. (H) *Pythium* sporangia with protoplasm differentiating into zoospores within vesicles.

then bottled and autoclaved for 15 minutes [Trione 1974]). Colonies are cultured in the dark for 3-5 days and then carefully and thoroughly rinsed with distilled water and flooded with soil extract water (SEW, equal amounts of soil and water mixed, left overnight at room temperature, and then filtered) for 8-12 hours in the dark to induce sporangia. Zoospores are often released during this period. Deciduous sporangia are detected by vigorously swirling flooded colonies. Deciduous (caducous) sporangia float free.

### Identification to Genus

The relatively slow growth of *Phytophthora* spp. makes their isolation from the many other fungi

of the root/soil environment difficult. The first challenge of identification is to separate *Phytophthora* from other fungi. Basically, all isolation procedures belong to two general categories: 1) baiting with seedlings or other plant tissues (Hamm and Hansen 1984, Linderman and Zeitoun 1977, McIntosh 1966, Ostrofsky *et al.* 1977, Roth pers. comm.); or 2) plating soil or infected tissue directly on selective media (Eckert and Tsao 1962, Pratt *et al.* 1976, Tsao and Ocana 1969). Fortunately the antibiotic Pimaricin (Delvicide 50% WP, GB Fermentation, Des Plaines, IL 60016) in all media prevents growth of most fungi except *Phytophthora* and *Pythium* (Eckert and Tsao, 1962). Another

### Key to *Phytophthora* Species Attacking Conifers in the Pacific Northwest.

- A<sub>1</sub> Zoospores liberated from vesicle attached to sporangium (Figure 1H) \_\_\_\_\_ *Pythium* spp
- A<sub>2</sub> Zoospores liberated directly from sporangium. (Figures 1C and D) \_\_\_\_\_ *Phytophthora* spp. \_\_\_\_\_ B
- B<sub>1</sub> Oogonia with predominantly (>50%) paragynous antheridia produced in single strain culture on clarified V-8 agar \_\_\_\_\_ C
  - C<sub>1</sub> Oogonia average >46  $\mu$ m \_\_\_\_\_ *P. megasperma* - Group 2
  - C<sub>2</sub> Oogonia average <44  $\mu$ m \_\_\_\_\_ D
    - D<sub>1</sub> Sporangia non-papillate and non-deciduous, ovoid or pear-shaped (length/width ratio usually large from 1.4:1.0 to 1.6:1.0) \_\_\_\_\_ *P. megasperma* - Group 1
    - D<sub>2</sub> Sporangia moderately to markedly papillate, nearly round (length/width ratio small, from 1.0:1.0 to 1.2:1.0) \_\_\_\_\_ E
      - E<sub>1</sub> Sporangia deciduous, markedly papillate, oogonia average 28  $\mu$ m, good growth (1-5 mm/day) on cornmeal agar at 30°C. \_\_\_\_\_ *P. cactorum*
      - E<sub>2</sub> Sporangia non-deciduous, moderately to markedly papillate, oogonia average 35  $\mu$ m, little or no growth (<1 mm/day) on cornmeal agar at 30°C. \_\_\_\_\_ *P. pseudotsugae*
- B<sub>2</sub> Oogonia with predominantly (>50%) amphigynous antheridia produced in single strain culture on clarified V-8 agar. Species with these characteristics have not been reported from Northwest conifers.
- B<sub>3</sub> Oogonia rarely produced in clarified V-8 agar in absence of opposite strain \_\_\_\_\_ F
  - F<sub>1</sub> Slow growing on cornmeal agar (2-4 mm/day at 20°C), isolated from *Chamaecyparis* species. \_\_\_\_\_ *P. lateralis*
  - F<sub>2</sub> Moderate to fast growing on cornmeal agar (4-9 mm/day at 20°C) \_\_\_\_\_ G
    - G<sub>1</sub> Mycelium with numerous small hyphal swellings. \_\_\_\_\_ *P. cinnamomi*
    - G<sub>2</sub> Mycelium without numerous hyphal swellings. \_\_\_\_\_ H
      - H<sub>1</sub> Colony appressed with dense rosettes of sharp, compact petals on clarified V-8 agar (Figure 2), and moderate growth (4-6 mm/day at 20°C) on cornmeal agar. \_\_\_\_\_ *P. drechsleri*
      - H<sub>2</sub> Colony aerial with slight or no pattern on clarified V-8 agar (Figure 2), and fast-growing (5-9 mm/day at 20°C) on cornmeal agar. Sporangia 37-55 x 23-30  $\mu$ m; oogonia smooth-walled in paired culture. \_\_\_\_\_ *P. cryptogea*
      - H<sub>3</sub> Colony aerial, without pattern on clarified V-8 agar, and moderate growth (4-6 mm/day) on cornmeal agar. Sporangia large (58-73 x 38-45  $\mu$ m); oogonia ornamented in paired culture. \_\_\_\_\_ *P. cambivora*

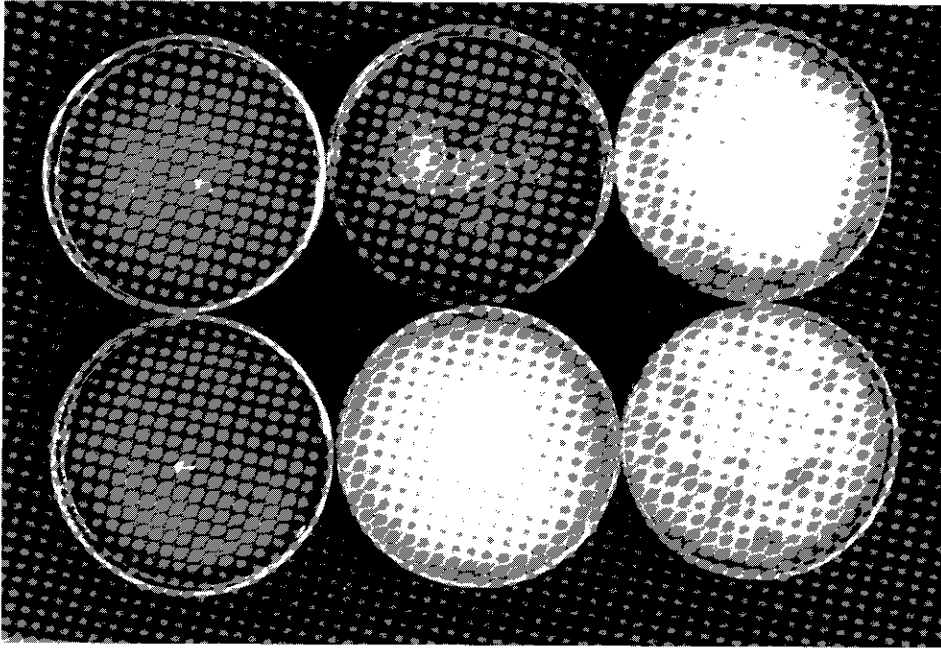


Figure 2. Growth characteristics of six *Phytophthora* species on clarified V-8 agar after 4 wks (top left to bottom right). *P. pseudotsugae*, *P. drechsleri*, *P. cinnamomi*, *P. lateralis*, *P. cryptogea* and *P. megasperma* Group I. Notice aerial growth of *P. cinnamomi*, *P. cryptogea* and *P. megasperma*.

antibiotic, hymexazol, restricts growth of some *Pythium* species without affecting most *Phytophthora* (Hansen *et al.* 1979, Masago *et al.* 1977, Tsao and Guy 1977).

*Pythium* and *Phytophthora* isolates can be distinguished by hyphal and colony characteristics, but sporangial characteristics are more reliable, and are also important for distinguishing among *Phytophthora* species. Thus, growing isolates first in pea broth, then inducing sporangia in SEW, will simultaneously separate *Pythium* from *Phytophthora*, and allow determination of sporangial characteristics of the *Phytophthora* species. Isolates should also be grown on clarified V-8 agar to obtain information on oogonia (size and antheridial attachment) and other structures (chlamydo spores or hyphal swellings), and on colony pattern. Growth rate on cornmeal agar (Difco) is also important for some species and should be determined prior to using the key. While all *Phytophthora* species known to be associated with Northwest conifers have been included, additional species may be isolated in the future. Therefore, as with any key, listed characteristics should be carefully considered to avoid mislabelling an unknown isolate.

### Diagnostic Characteristics by Species

The following list includes characteristics that are especially helpful in identification of *Phytophthora* species recovered from Pacific Northwest conifers. Consult other sources (Newhook *et al.* 1978; Waterhouse 1963, 1970) for complete descriptions.

#### *Phytophthora cactorum*

A variable species worldwide, *P. cactorum* most closely resembles *P. pseudotsugae* in the Pacific Northwest. Sympodial production of ovoid to obpyriform, papillate, deciduous sporangia (size range 36-50 x 28-35  $\mu$ m) on solid and liquid media is characteristic. *P. cactorum* usually produces abundant oogonia (size range 25-32  $\mu$ m, generally smaller than *P. pseudotsugae*) with paragynous antheridia and mature oospores.

Chlamydo spores are rarely formed. Unlike *P. pseudotsugae*, *P. cactorum* rots apple fruits within two weeks when a small agar plug containing the fungus is inserted into a hole made by a cork borer and covered with tape. *P. cactorum* causes root rot of Douglas-fir (*Pseudotsugae*

*menziesii*) and true fir (*Abies* sp.) in Oregon and Washington forest tree nurseries. It is also an important pathogen of certain orchard and ornamental crops in this region.

#### *Phytophthora cambivora*

This species is heterothallic, moderate-fast growing and patternless with aerial mycelium on clarified V-8 agar. *P. cambivora* generally grows more slowly than *P. cryptogea*, and produces larger sporangia (58-73 x 38-45  $\mu$ m), and oogonia (39-51  $\mu$ m). Oogonia are distinctly ornamented and antheridia commonly are two-celled. It lacks the numerous hyphal swellings and chlamydo-spores of *P. cinnamomi* on clarified V-8 agar.

*P. cambivora* is best known in the Northwest as a root and collar pathogen of fruit trees. This species was recently isolated from dead roots and girdling stem cankers on 2-5 year old Noble fir in a number of Christmas tree plantations in Oregon, but pathogenicity has not yet been confirmed (P. B. Hamm and G. A. Chastagner, unpublished data).

#### *Phytophthora cinnamomi*

This species, like *P. lateralis*, readily produces chlamydo-spores (average 41  $\mu$ m) in culture. *P. cinnamomi* grows much faster on cornmeal agar than *P. lateralis* (4-8 versus 1-2 mm/day respectively, at 20°) and has numerous hyphal swellings (Figure 2g). Sporangia (size range 27-114 x 20-71  $\mu$ m) are persistent, non-papillate, ellipsoid to ovoid and form on unbranched sporangiophores. Oogonia, with amphigynous antheridia (size range 21-58  $\mu$ m), form only in paired culture.

*P. cinnamomi* has been known to cause extensive damage to Douglas-fir only once in a Pacific Northwest forest tree nursery (Kanaskie pers. comm.). Damage has also been seen in rooted cuttings of Douglas-fir before and after transplanting in seed orchards and in Noble fir grown for Christmas trees. This species affects a wide number of ornamental plant species in this region, including *Taxus*, *Chamaecyparis*, *Pseudotsuga*, *Abies*, and other conifers (see Zentmyer 1980).

#### *Phytophthora cryptogea*

This species is fast growing, heterothallic, and produces a patternless, aerial colony on clarified

V-8 agar (Figure 2). Hyphal swellings and chlamydo-spores are not produced. Sporangia are smaller than *P. cambivora* (range 37-55 x 23-30  $\mu$ m) they are non-papillate, persistent, and ovoid. Oogonia are smooth walled and smaller (30-38  $\mu$ m) than *P. cambivora*, having a single-celled amphigynous antheridium.

*P. cryptogea* has caused root rot of Douglas-fir in British Columbia, Washington and Oregon nurseries, true fir in Washington nurseries and in Oregon Christmas tree plantations, and sugar pine (*Pinus lambertiana*) in a Southern Oregon seed orchard.

#### *Phytophthora drechsleri*

*P. drechsleri* occasionally produces sporangia in solid media in isolation plates, a characteristic similar to *P. cactorum*. Chlamydo-spores form infrequently compared to *P. lateralis* or *P. cinnamomi*. The radiating, strongly rosette pattern of the colony formed on clarified V-8 agar is distinctive (Figure 2). Sporangia (size range 36-70 x 26-40  $\mu$ m) are nonpapillate, persistent, and elongated, produced on sympodially branched sporangiophores. Oogonia (size range 36-53  $\mu$ m) with amphigynous antheridia form only when colonies are paired with isolates of the opposite mating type.

*P. drechsleri* has been isolated from Douglas-fir in British Columbia, Oregon, and Washington nurseries, from forest soil in southeast Alaska and southwest Oregon, and from Noble fir Christmas trees in Oregon.

#### *Phytophthora lateralis*

Though placed here with heterothallic species to ease identification, *P. lateralis* is homothallic, forming oogonia only after 8-12 wks in Port-Orford-cedar foliage extract agar (Trione 1974). Growth rate at optimum temperature (2-3 mm/day at 20°) is the slowest of all *Phytophthora* species from conifers in this region. Sporangia on sympodially branched sporangiophores are persistent, non-papillate and mostly ovate or pyriform averaging 59 x 35  $\mu$ m. Oogonia (size range 33-50  $\mu$ m) have paragynous antheridia. Large numbers of chlamydo-spores (average size 40  $\mu$ m) often form in clarified V-8 agar. Apple fruits are rotted very slowly or not at all.

*Phytophthora lateralis* reportedly attacks trees in the genus *Chamaecyparis* exclusively

(Torgeson *et al.* 1954). Port-Orford-cedar (*Chamaecyparis lawsoniana*), a tree native to southwest Oregon and northwest California, has been planted extensively as an ornamental throughout western Oregon, Washington, and British Columbia, and mortality from *P. lateralis* has been reported in each of these areas. The fungus is highly destructive in the forest.

#### *Phytophthora megasperma* Group 1

*P. megasperma* is a variable species worldwide with a number of distinct subgroups. Two subgroups, differing in morphology, growth characteristics, pathogenicity, host range, and response to metalaxyl (a very specific fungicide), have been recovered from Douglas-fir nursery stock in Oregon. Oogonia of isolates belonging to Group 1 average  $<44 \mu\text{m}$  in size, are not as pigmented on clarified V-8 agar as those from Group 2, and are generally produced in large numbers. Optimum growth occurs at 27°C, but isolates also grow well (1-2 mm/day) at 35°C. Isolates from Group 1 are inhibited (80% growth reduction) by metalaxyl (*in vitro*) at 1  $\mu\text{g/ml}$  (Hansen and Hamm 1983, Hunger *et al.* 1982). Isolates of *P. megasperma* Group 1 are more aggressive in pathogenicity studies than *P. megasperma* Group 2 (Hamm and Hansen 1981, 1982a). Sporangia on unbranched sporangio-phores (average size  $53 \times 35 \mu\text{m}$ ) are persistent, non-papillate, and mostly ovoid. Oogonia with predominantly paragynous antheridia form in single-strain culture. Chlamydo-spores are lacking.

*Phytophthora megasperma* Group 1 has been found killing Douglas-fir roots in only one Oregon forest nursery.

#### *Phytophthora megasperma* Group 2

Oogonia average  $>46 \mu\text{m}$  in size, are usually distinctly pigmented light or yellow-brown and generally are not produced in large quantities on clarified V-8 agar. Optimum growth temperature

is 22°C. The fungus will not grow at 35°C. Growth inhibition (*in vitro*) by metalaxyl at 1  $\mu\text{g/ml}$  is 45% (Hansen and Hamm 1983, Hunger *et al.* 1982). Sporangial characteristics are similar to those of *P. megasperma* Group 1.

*P. megasperma* Group 2 has been found on Douglas-fir in Washington and Oregon nurseries, and on true fir and sugar pine only in Oregon nurseries. Group 2 isolates of *P. megasperma* are not as aggressive on Douglas-fir as isolates from Group 1 (Hamm and Hansen 1981, 1982a).

#### *Phytophthora pseudotsugae*

This species, closely resembling *P. cactorum*, differs by producing larger oogonia (average size  $>32 \mu\text{m}$ ), oospores that often abort, persistent papillate sporangia (average size  $39 \times 32 \mu\text{m}$ ) produced rarely in solid media and infrequently in liquid media, and has a lower optimum temperature for growth (20-25 versus 25-27°C for *P. cactorum*).

*P. pseudotsugae* does not produce pigment on casein hydrolysate-tyrosine medium, is sensitive to malachite green, and in contrast to *P. cactorum*, does not decay apple fruits (Hamm and Hansen 1983, Ho 1981). *Phytophthora pseudotsugae* rarely forms hyphal swellings, does not form chlamydo-spores, and nearly always has paragynous antheridia.

*Phytophthora pseudotsugae* has been found only in Oregon and Washington forest nurseries where it attacks Douglas-fir seedlings.

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