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Address manuscripts and proofs to:
Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

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Cover Illustration

An original drawing, seemingly the only one surviving and perhaps the only one ever done for publication by Merritt Lyndon Fernald, used in part to illustrate his article on cranberry species which appeared in RHODORA No. 48 (Fernald, M. L. 1902. The variations and distribution of American cranberries. Rhodora 4: 231–237 & Plate 40). The drawing was rescued from a wastebasket by Dr. Bernice Schubert; it now hangs in the office of Dr. Carroll E. Wood at GH. The original Plate 40 caption reads as follows: Fig. 1, *Vaccinium Vitis-Idaea;* fig. 2, *V. Vitis-Idaea,* var. *minor;* fig. 3, *V. Oxycoccus;* fig. 4, *V. Oxycoccus* var. *intermedium;* fig. 5, *V. macrocarpon.*

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A SYNOPSIS OF NEW HAMPSHIRE SEAWEEDS[1,2]

ARTHUR C. MATHIESON AND EDWARD J. HEHRE[3]

ABSTRACT

Species composition, phenology, longevity and distribution patterns of New Hampshire seaweed populations from diverse coastal and estuarine habitats are given. Two hundred sixteen taxa were recorded (58 Chlorophyceae, 66 Phaeophyceae and 92 Rhodophyceae), including 8 new state and/or geographical records and the recent introduction of the green alga *Codium fragile* subsp. *tomentosoides* to the Isles of Shoals. Each major group of seaweeds showed similar phenological patterns, with summer maxima and winter minima. The Rhodophyceae exhibited the greatest dominance by perennials (67.4%), the Phaeophyceae had an intermediate pattern (45.5%) and the green algae exhibited the greatest dominance by annuals (87.2%). Overall, the open coastal sites were dominated by cold temperate species, while warm temperate or "mixed floras" were more conspicuous in estuarine habitats. Varying phenological and longevity patterns were also evident in coastal and estuarine habitats. Most of the species (67%) occurred in both open coastal and estuarine habitats, while 23% were restricted to the open coast and 7% to estuarine habitats. Several unique distributional patterns were also noted, including contrasting patterns between closely related taxa, parasitic species and their respective hosts, and different life history stages of the same species. Several estuarine taxa represent disjunct populations north of Cape Cod, Massachusetts; they may be relicts of an earlier "hypsithermal" or warm period. The autecology of several disjunct taxa is discussed.

Key Words: seaweeds, coastal, estuarine, phenology and distribution, New Hampshire

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[1] Scientific Contribution Number 1359 from the New Hampshire Agricultural Experiment Station; also issued as Contribution Number 130 from the Jackson Estuarine Laboratory.

[2] This paper is dedicated to Dr. Robert F. Scagel on the occasion of his academic retirement and in recognition of his outstanding and pioneering efforts in marine phycology, particularly of the Pacific Northwest.

[3] Present address: 26 Park Street, South Berwick, Maine 03908

INTRODUCTION

Until recently there have been few published accounts of New Hampshire (Figures 1–4) seaweeds. Farlow (1882) and Collins (1900, 1901, 1903 and 1906a) compiled the earliest records for the state; subsequently, Croasdale (1941) listed a few additional records, primarily from the Isles of Shoals (Figure 2). Wood and Straughan (1953) described the penetration of the freshwater red alga *Sacheria fucina* (as *Lemanea fucina*) within the tidal portions of the Oyster River (Figure 3). Doty and Newhouse (1954) recorded several collections from the Great Bay Estuary System (Figure 3) and noted a conspicuous decrease in species numbers from the mouth to the head of the estuary. Taylor (1957) summarized many of the earlier records for New Hampshire and adjacent New England states in his excellent account of the benthic marine flora of northeastern North America.

Since 1965, a variety of floristic, phenological and ecological studies of New Hampshire's (Figures 1–4) marine algal flora have been conducted by phycologists at the University of New Hampshire. Hehre and Mathieson (1970) described the species composition, seasonal occurrence and reproductive periodicity of 88 taxa of red algae from various open coastal and estuarine environments. Similar floristic and phenological data were recently summarized on the Phaeophyceae (Mathieson and Hehre, 1982) and Chlorophyceae (Mathieson and Hehre, 1983). The seasonal occurrence and vertical distribution of 125 seaweeds at Jaffrey Point (Fort Stark), New Castle, New Hampshire were recorded (Mathieson, Hehre and Reynolds, 1981), as well as the distributional patterns of marine algae within the Great Bay and Hampton-Seabrook (Figures 3 and 4) estuary systems (Mathieson, 1975; Mathieson and Fralick, 1972; Mathieson, Reynolds, and Hehre, 1981). Each of the estuarine areas showed a "typical" reduction pattern inland, as well as the importance of tidal rapids in determining local and discontinuous distributional patterns. A comparison of the species composition of seaweeds from the Merrimack River estuary (Figure 1), Massachusetts, (Mathieson and Fralick, 1973) with that of the Hampton-Seabrook and the Great Bay estuary systems (see earlier citations) indicates a paucity of total species and number of taxa/station in the Merrimack River estuary—one of the most polluted rivers in New England (Jerome et al., 1965; Miller et al., 1971). In contrast, tidal

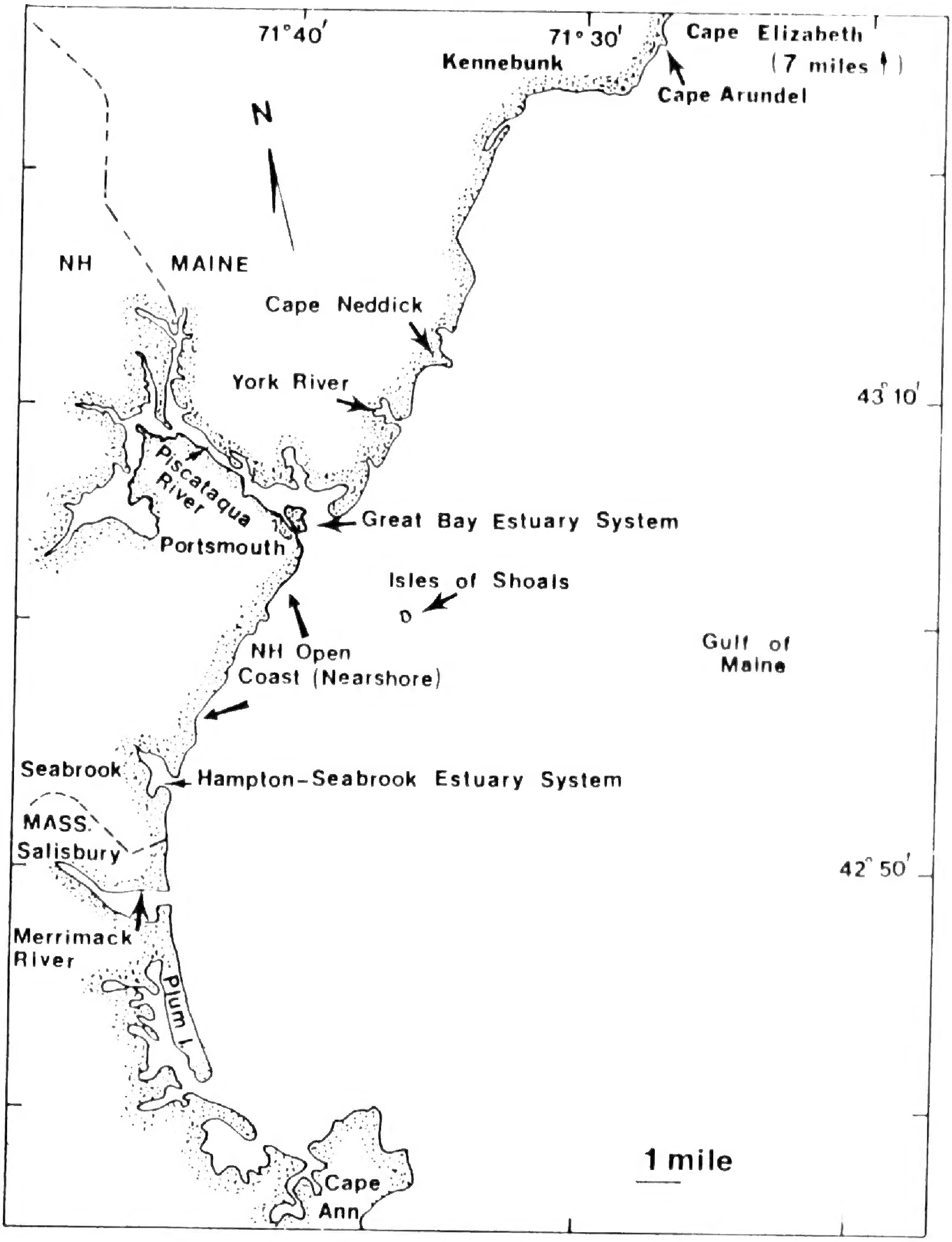

Figure 1. The New England coastline between Cape Arundel, Maine and Cape Ann, Massachusetts, including the four primary coastal-estuarine areas within New Hampshire.

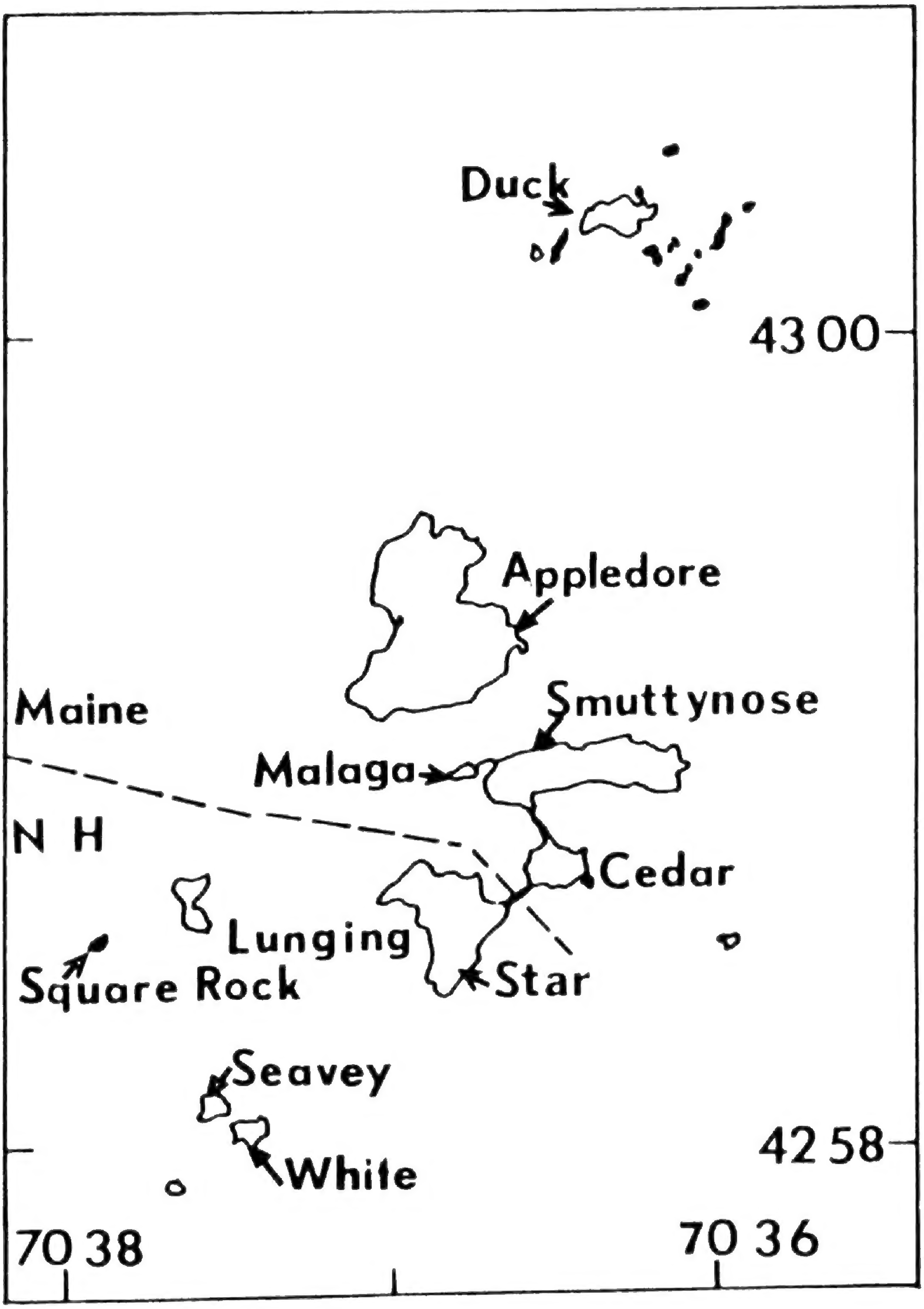

Figure 2. The Isles of Shoals, New Hampshire–Maine.

rapid sites such as Dover Point, which occur within the Great Bay Estuary System (Figure 3), can exhibit a much greater diversity of species than the entire Merrimack River (Mathieson, Neefus and Emerich Penniman, 1983; Mathieson and Fralick, 1973; Reynolds and Mathieson, 1975). Tidal rapids also exhibit a more diverse flora than adjacent "back-eddy" sites, and such rapids may represent major phytogeographic boundaries within estuaries (Mathieson, Reynolds and Hehre, 1981).

A comparative phytogeographic evaluation of seaweed populations at the Isles of Shoals (Figure 2), an archipelago of eight major offshore islands near southern Maine and New Hampshire, showed that the mean similarity within the Shoals was approximately 82% and that a significant proportion of the variance in species richness per island was explained by the length of semi-exposed shoreline on each island (Mathieson and Penniman, 1986a). Detailed studies of the subtidal flora of New Hampshire were initiated by SCUBA diving on the open coast and within the Great Bay Estuary System (Mathieson, 1975, 1979; Mathieson and Burns, 1970; Mathieson, Hehre and Reynolds, 1981). The species richness, longevity and vertical distribution of the subtidal seaweed populations were related to a variety of environmental parameters, including temperature, salinity, light and water motion. Additional descriptive accounts of New Hampshire algae have been given by Normandeau Associates (1971–1980) for the Piscataqua River near the Schiller Power Plant, by the New Hampshire Department of Fish and Game (Nelson et al., 1981, 1982) for the Great Bay Estuary System, and by Daly and Mathieson (1977) at Bound Rock in Seabrook. Several additional biosystematic (Blair, 1983; Blair et al., 1982), floristic (Hehre, 1972) and autecological investigations of New Hampshire seaweeds have been conducted (Burns and Mathieson, 1972a, b; Chock and Mathieson, 1976, 1983; Daly and Mathieson, 1977; Hardwick-Witman and Mathieson, 1983; Josselyn and Mathieson, 1978, 1980; Kilar and Mathieson, 1978, 1981; Mathieson, 1979, 1982a; Mathieson and Burns, 1975; Mathieson, Neefus and Emerich Penniman, 1983; Mathieson, Penniman, Busse and Tveter-Gallagher, 1982; Mathieson and Prince, 1973; Mathieson, Shipman, O'Shea and Hasevlat, 1976; Niemeck and Mathieson, 1976; Norall et al., 1981; Sideman and Mathieson, 1983a, b, 1985; Tveter and Mathieson, 1976; Tveter-Gallagher and Mathieson, 1980; Tveter-

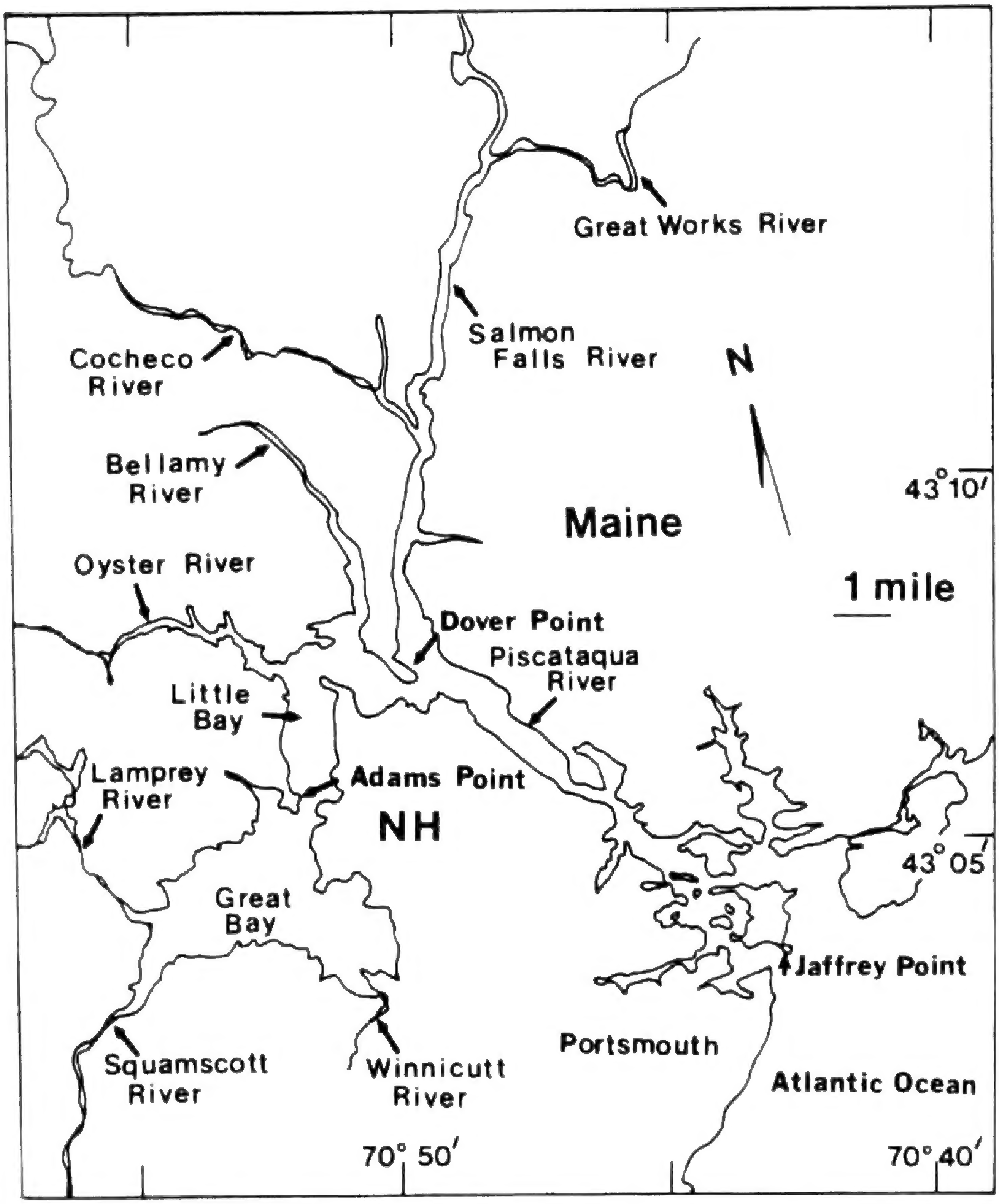

Figure 3. The Great Bay Estuary System and the adjacent open coast of New Hampshire-Maine.

Gallagher, Mathieson and Cheney, 1980; Zechman and Mathieson, 1985).

In the present account, a synopsis of the Chlorophyceae, Phaeophyceae and Rhodophyceae from coastal/estuarine habitats in New Hampshire is given, based upon a synthesis of the above-described collections and data. The phenology, longevity and local distribu-

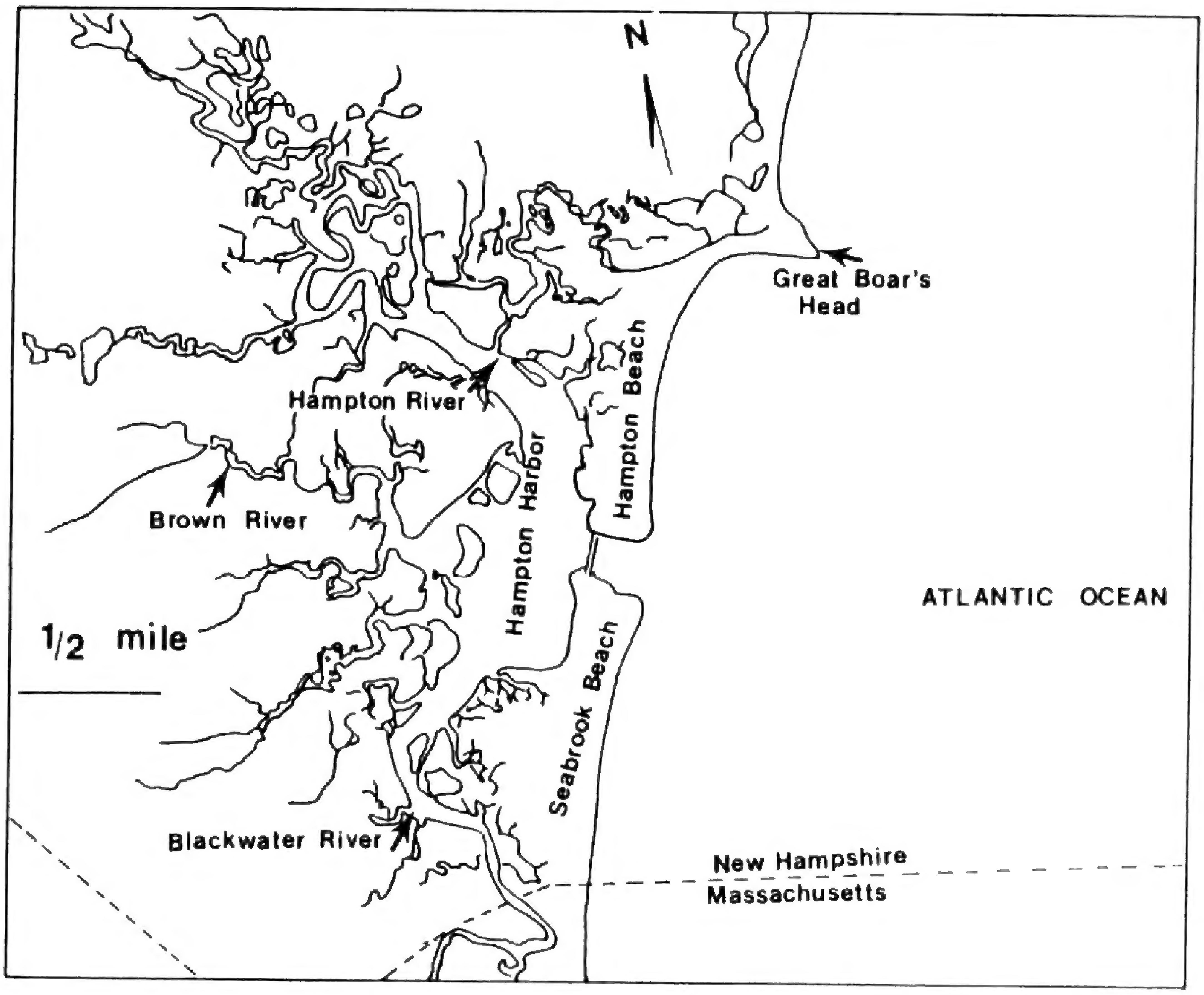

Figure 4. The Hampton-Seabrook Estuary System and the adjacent open coast of New Hampshire and Massachusetts.

tional patterns of each taxon are summarized in a series of detailed distribution maps. Norton (1978), among others, has emphasized that distributional maps are significant tools in marine ecology, particularly if a comprehensive set of environmental data is available. A detailed synopsis of the New Hampshire coastal zone is given to aid in such geographical and ecological comparisons.

METHODS AND MATERIALS

As outlined previously, extensive collections and observations of New Hampshire seaweeds have been made at a variety of open coastal and estuarine sites (Figure 5, Table IV and Appendix) during 1965–83 in order to prepare a detailed synopsis of the state's marine algal flora. Thus, collections were made at 212 study sites,

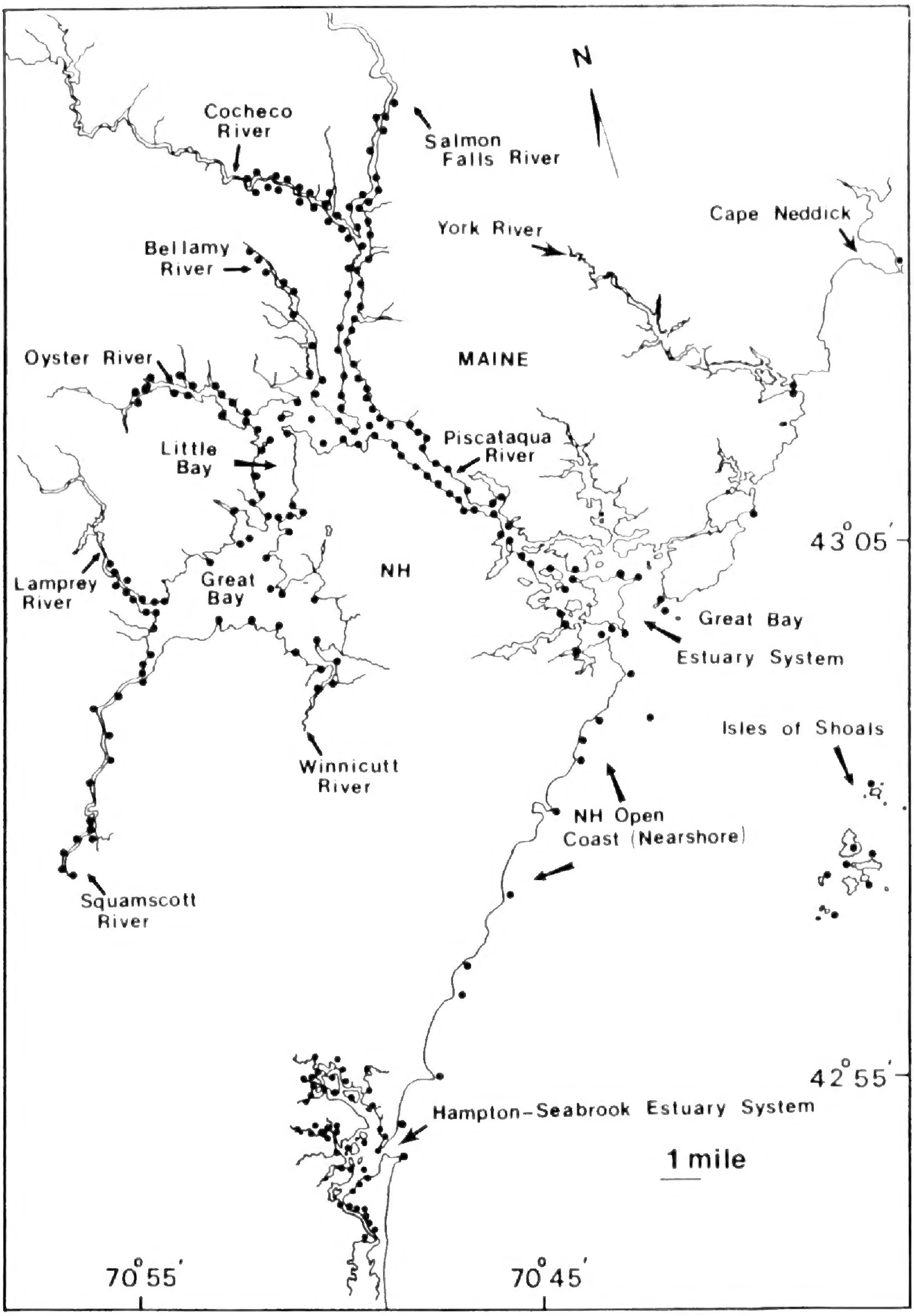

Figure 5. Summary of 256 collecting sites in New Hampshire and southern Maine.

including 23 locations where a minimum of 2 years of monthly collections were made. Forty-nine stations were studied in the Hampton-Seabrook Estuary, New Hampshire, during the summer and fall of 1969 (Mathieson and Fralick, 1972), including collections from the five major rivers and creeks, Hampton Harbor and the adjacent open coast near Hampton. Thirteen sites from the nearshore open coast between Portsmouth and Seabrook were documented, as well as the species composition at three of the nine major islands at the Isles of Shoals (Mathieson and Penniman, 1986a). One hundred forty-seven collection sites were studied within the Great Bay Estuary System, including Great Bay, Little Bay, the Bellamy, Cocheco, Lamprey, Oyster, Piscataqua, Salmon Falls, Squamscott and Winnicut Rivers. Collections were also made at 44 adjacent coastal and estuarine sites in Maine (Figure 5, Table IV and Appendix).

Representative samples of all conspicuous species at each site (Table IV and Appendix) were made in the littoral (on foot) and sublittoral zones (by SCUBA). Methods of collection, identification and processing of samples were similar to those outlined by Hehre and Mathieson (1970) and Mathieson, Hehre and Reynolds (1981). Monthly collections for at least 2 years were made at 23 sites ranging from the nearshore open coast of New Hampshire through the entire Great Bay Estuary System, including its tidal tributaries (Table IV and Appendix). Intermittent or seasonal collections were made at the other 233 sites (i.e., including 44 Maine stations). Herbarium voucher specimens of each taxon/site were prepared and deposited in NHA. The complete set of approximately 40,000 specimens is deposited in order to document temporal and spatial characteristics of the state's marine algal flora. The primary source of identification was Taylor (1957); even so, several other monographs (*see* Mathieson, Hehre and Reynolds, 1981, for a partial listing) and the recent nomenclatural changes summarized by South (1984) were also employed.

THE NEW HAMPSHIRE COASTAL ZONE

The New Hampshire coastline is located approximately midway between Cape Elizabeth, Maine, and Cape Ann, Massachusetts

(Figure 1). Many geological-topographical characteristics are common to this coastal region, including the general absence of offshore islands, the presence of sandy barrier beaches in front of extensive salt marshes, and the occurrence of large rocky headlands or promontories.

As shown in Figures 1–4, the state's coastal zone consists of four primary areas:

1. Isles of Shoals
2. seventeen miles of nearshore open coast and adjacent salt marshes
3. Hampton-Seabrook Estuary System
4. Great Bay Estuary System

The Isles of Shoals are located approximately 9 miles SSE of the mouth of the Piscataqua River and 6.5 miles due east of Straw Point, Rye (Figures 1 and 2). The islands oocupy an area 3 miles north-south by 1.5 miles east-west and lie between the coordinates 42°59′N, 70°37′20″W and 43°00′30″N, 70°36′W. There are nine major islands: five are under the jurisdiction of the Town of Kittery, Maine (Appledore, Cedar, Duck, Malaga, and Smuttynose), and four are within Rye, New Hampshire (Lunging, Seavey, Star and White). Nine other rocks and ledges are present in the Island group (Anderson, Eastern, Halfway, Mingo, Shag and Square Rocks, plus Cedar and White Islands Ledges and Southwest Ledge). The Isles of Shoals are massive granitic outcrops, the north and east sides of which are exposed to extreme wave action, particularly during storms. The west and south sides of the islands are more sheltered, such as, Gosport Harbor on the leeward side of Star Island. Mathieson and Penniman (1986a) and Norall et al. (1981) give a variety of other details regarding the physical-environmental characteristics of the Shoals.

The southern boundary of New Hampshire's nearshore open coast (Figures 1 and 4) is at Seabrook (42°52′30″N, 70°49′W), while the northern boundary is at the mouth of the Piscataqua River near the entrance to Portsmouth Harbor (43°04′20″N, 70°42′42″W). Extensive salt marshes occur along this coast, particularly near Rye, Portsmouth and Hampton. Three major habitats are found on the nearshore open coast: cobble-boulder, exposed headlands, and sandy beaches (*see* Hehre and Mathieson, 1970, for further descriptions). The metamorphic headlands at Rye Ledge and Great Boars

Head are exposed to extreme wave action. The most extensive sandy beaches are found in the Hampton and Seabrook areas.

The Hampton-Seabrook Estuary (Figure 4) is located entirely within the State of New Hampshire, between latitudes 42°51′30″N to 42°55′55″N and longitudes 70°49′30″W to 70°51′30″W. This estuary is within the townships of Hampton, Hampton Falls and Seabrook, and has a total area of about 3,800 acres. Five rivers (Taylor, Hampton, Hampton Falls, Brown and Blackwater), as well as a variety of smaller creeks and brooks are present within this estuary.

The Great Bay Estuary System occurs within New Hampshire and Maine (Figure 3). It consists of Great Bay, Little Bay, the Piscataqua River, Portsmouth Harbor and its tributaries, as well as seven other freshwater rivers (Bellamy, Cocheco, Lamprey, Oyster, Salmon Falls, Squamscott and Winnicut), which drain into the basin. The Great Bay Estuary System is one of the largest estuaries on the eastern seaboard of the United States, with over 11,000 acres of tidewater (Anon., 1960). The total drainage area of the estuary is approximately 930 square miles, two-thirds of which is within New Hampshire (Anon., 1960). The estuary contains about 100 miles of shoreline. The substratum in the Great Bay Estuary System, as well as the Hampton-Seabrook Estuary, is dominated by mud (Hardwick-Witman and Mathieson, 1983); occasional rock outcrops, cobbles, shells and artificial structures such as pier pilings are also present. Overall, the substratum within the Hampton-Seabrook Estuary is more sandy than the Great Bay Estuary System, particularly toward Hampton Harbor.

The seasonal patterns of surface water temperatures on the nearshore open coast of New Hampshire and within the Great Bay Estuary System are illustrated in Figure 6. Typically, the maximum temperatures occur during mid-summer through the fall. Thereafter, temperatures decrease rapidly, particularly in the inner estuary, with lowest values occurring January to March. Open coastal site have a narrower temperature range than estuarine sites. For example, surface water temperatures at the Isles of Shoals vary from 3.8° to 18.2°C, versus −1.0° to 19.0°C at Portsmouth Harbor, −2.0° to 24.1°C at Dover Point, −1.8° to 26.5°C at Adams Point, and −2.0° to 27.0°C within Great Bay proper (Emerich Penniman et al., 1985; Norall and Mathieson, 1976; Norall et al., 1982). Even

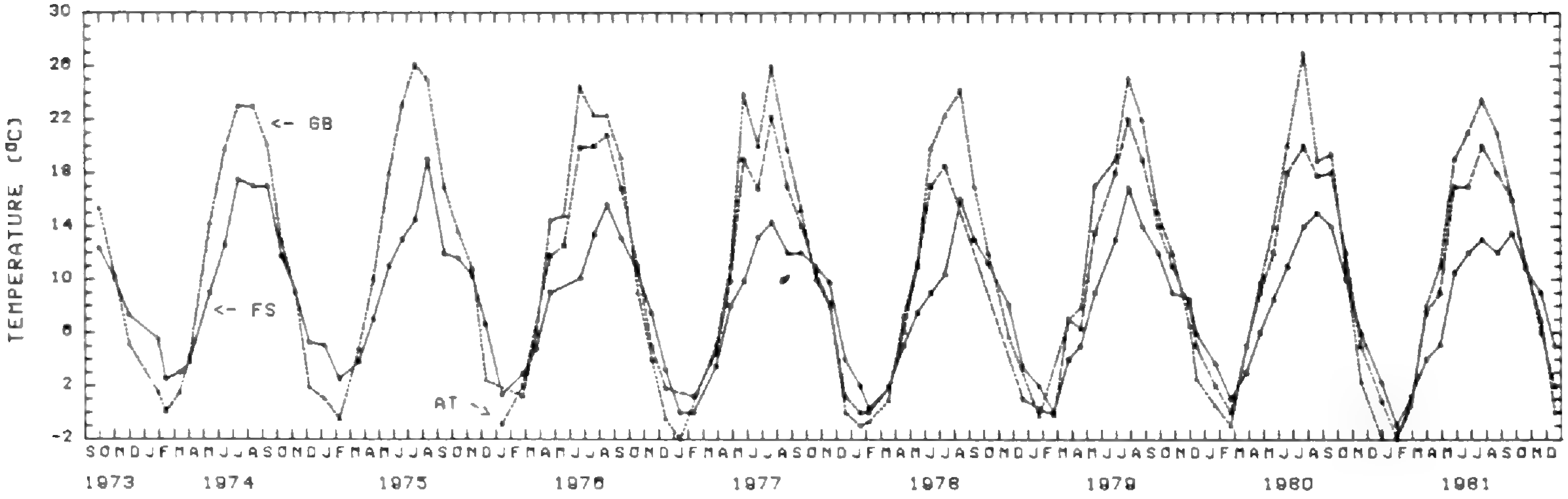

Figure 6. Seasonal variation of surface water temperature on the nearshore open coast of New Hampshire (Jaffrey Point, Fort Stark) and within the Great Bay Estuary System (Atlantic Terminal and Great Bay) during 1973 1981 (based upon Emerich Penniman et al., 1985).

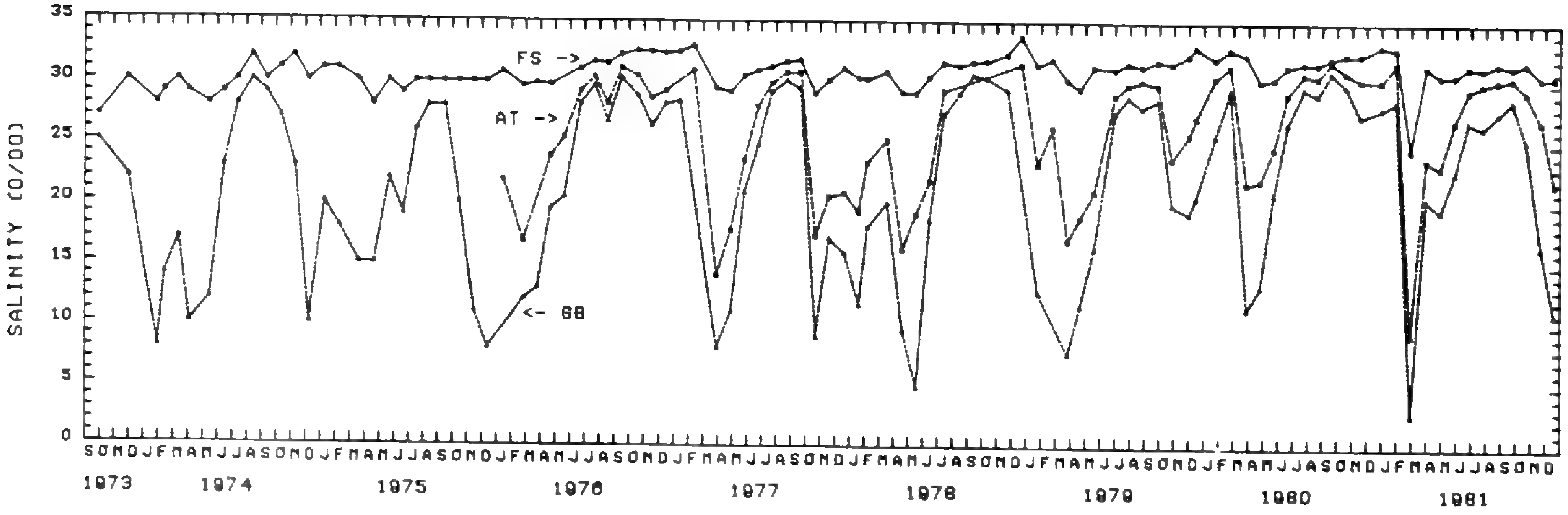

Figure 7. Seasonal variation of surface water salinities on the nearshore open coast of New Hampshire (Jaffrey Point, Fort Stark) and within the Great Bay Estuary System (Atlantic Terminal and Great Bay) during 1973–1981 (based upon Emerich Penniman et al., 1985).

greater variations (daily and seasonally) of temperatures are present within riverine habitats of the Great Bay Estuary System. Daly and Mathieson (1979, 1981), Daly et al. (1979), Emerich Penniman et al. (1985), Glibert (1976), Loder et al. (1979), Norall and Mathieson (1976), Norall et al. (1982), and Silver and Brown (1979) all gave details regarding temperature and salinity variations within the same geography. Overall, there is a pattern of greater variation as well as increasing mean surface water temperatures from the open coast to the inner estuary (Figure 8).

The seasonal patterns of surface water salinities on the nearshore open coast of New Hampshire and within the Great Bay Estuary System are illustrated in Figure 7. Typically, the maximum salinities occur in the summer and fall, while the lowest salinities occur during January to early spring—i.e., during winter and spring thaws. As with temperatue, the most pronounced salinity variations occur within inner estuarine sites, while adjacent open coastal areas are more stable. For example, the surface water salinities at the Isles of Shoals range from 31.0–33.0‰, while greater variations are evident at Portsmouth Harbor (24.6–33.8‰), Dover Point (0.9–30.3‰), Adams Point (6.6–31.4‰), and within Great Bay proper (2.7–30.97‰) (Emerich Penniman et al., 1985; Norall and Mathieson, 1976; Norall et al., 1982). Overall, there is a pattern of increased salinity variation (daily and seasonally), as well as a clinal decrease in surface water salinities, from the open coast of New Hampshire to the inner estuary (Figure 8).

A foot or more of ice is usually present from late December to March in Great Bay and the major tidal rivers (except the Piscataqua) within the Great Bay Estuary System. The scouring effects of ice are evident on rocks, pier pilings and other solid substrata. Large sections of marshy shoreline may be torn loose (rafted) during the spring thaw (Hardwick'Witman, 1985; Mathieson, Penniman, Busse and Tveter-Gallagher, 1982). Floating ice rafts and icebergs can often be seen on the adjacent open coast (Jaffrey Point) during the spring thaw.

The water transparency at the Isles of Shoals is much greater than in Portsmouth Harbor, which in turn is greater than that within the Great Bay Estuary System (Daly et al., 1979). The depth of penetration of light (1%) in the sea determines the lower limits of plant distribution along this natural gradient (Figure 8). Thus, attached

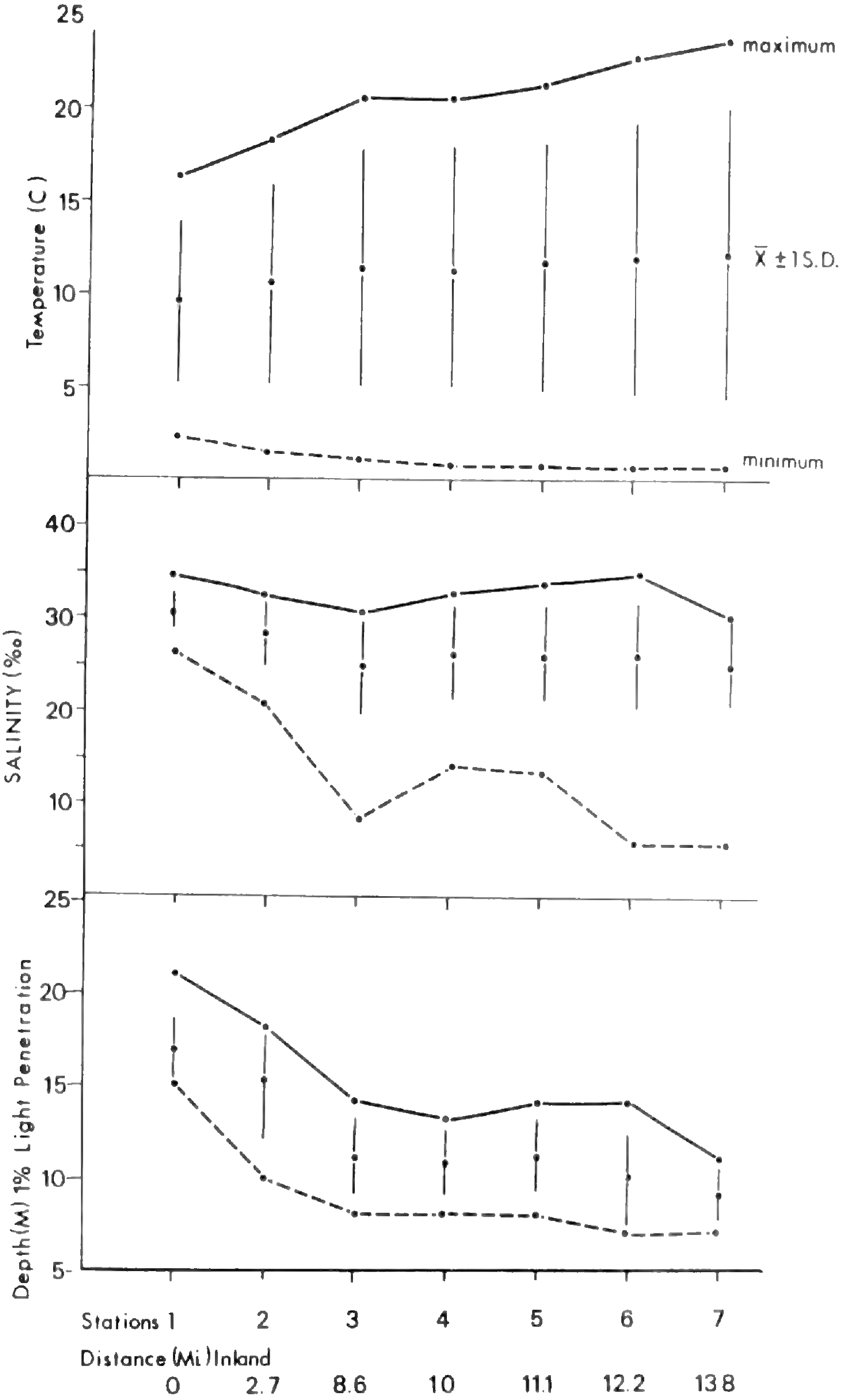

Figure 8. Mean values of surface water temperatures, salinities and 1% light penetration on the nearshore open coast of New Hampshire and within the Great Bay Estuary System during 1974–1978 (based upon Daly et al., 1979).

marine plants which require light to photosynthesize are found at 100–125 feet at the Shoals, 60–80 feet near the mouth of Portsmouth Harbor, and 10–15 feet in the upper parts of Great Bay proper (Figure 9). The differential water clarity of the estuary is primarily related to the volume of silt and organic material (detritus) in the latter habitat (Daly et al., 1979; Norall and Mathieson, 1976; and Norall et al., 1982).

Differential levels of nutrients (nitrogen and phosphorus) are evident on the open coast of New Hampshire and within the Great Bay Estuary System (Figures 10 and 11), with lower values occurring in the former areas (Norall and Mathieson, 1976; Norall et al., 1982). In general, nutrients are highest during the winter months from December into March; thereafter, a sharp decline occurs due to the spring bloom of phytoplankton. Intermediate levels are usually found during the summer, and they begin to increase during the fall. A detailed tabulation of seasonal and spatial variations of ni-

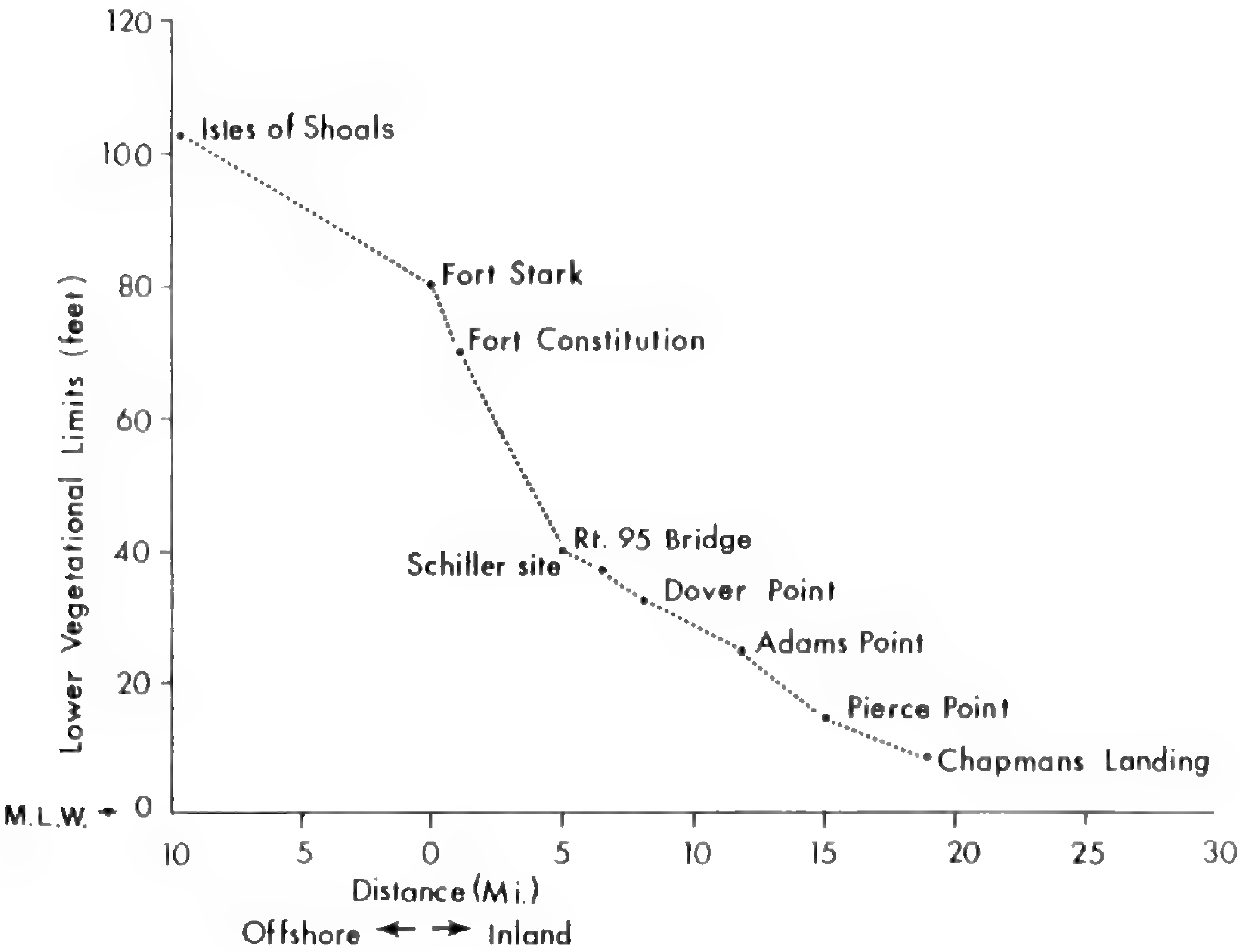

Figure 9. The lower limits of subtidal plant distribution between the Isles of Shoals and the inner reaches of the Great Bay Estuary System.

trogenous, phosphorous, and silicious nutrients within the Great Bay Estuary System and the adjacent open coast of New Hampshire is given by Norall and Mathieson (1976), Norall et al. (1982), and Emerich Penniman et al. (1985). Additional nutrient data for the same area are summarized by Burns and Mathieson (1972b), Glibert (1976), Loder and Glibert (1977, 1980), Loder et al. (1979), Lyons, Loder and Murray (1982), Mathieson and Burns (1975) and Mathieson and Tveter (1975).

The average tidal amplitude at the Shoals and near Portsmouth Harbor is about 8.1 feet, while it is about 6.8 feet at the head of Great Bay proper (Anon., 1965). Two high and two low tides occur each day in the coastal zone, and they are uniformly semi-diurnal. Tides cause considerable fluctuations of water transparency, temperature, salinity and current speeds, particularly in estuarine habitats (Daly and Mathieson, 1979). Tidal currents are a conspicuous feature of the Great Bay Estuary System (Figure 3), particularly in narrow channels near Adams Point, Dover Point, Fox Point, and the lower Piscataqua River (Brown and Arrellano, 1979; Celikkol and Reichard, 1976; Mathieson, Neefus, and Emerich Penniman, 1983; Mathieson, Reynolds, and Hehre, 1981; Mathieson, Tveter, Daly and Howard, 1977; Reynolds and Mathieson, 1975; Schmidt, 1980; Swenson et al., 1977; Trask and Brown, 1980). In such habitats tidal currents of 4–6 knots are evident, with maximum currents occurring during ebb tide (Figure 12). All of the tidal waters of the Great Bay Estuary System enter and leave via the Piscataqua River, creating strong tidal currents.

Domestic pollution is moderate within the Great Bay Estuary System. Treated effluent (chlorinated and settled) is discharged from the towns of Dover, Durham, Exeter, Newmarket and Rochester. Occasionally, raw sewage may be discharged during extreme storm periods when some sewage treatment plants (Dover) cannot handle the volume. Industrial pollution (heavy metals and organic sludge) is discharged from Dover, Rochester and Portsmouth (Capuzzo and Anderson, 1973; Hines et al., 1984; Lyons, Armstrong, O'Neil and Gaudette, 1982). Little industrial pollution occurs in the Hampton-Seabrook Estuary. On the open coast of New Hampshire, little pollution from domestic and industrial sources occurs, except for a few "point sources" of domestic discharges in Rye and other areas. The Isles of Shoals represent a relatively "pristine" coastal environment.

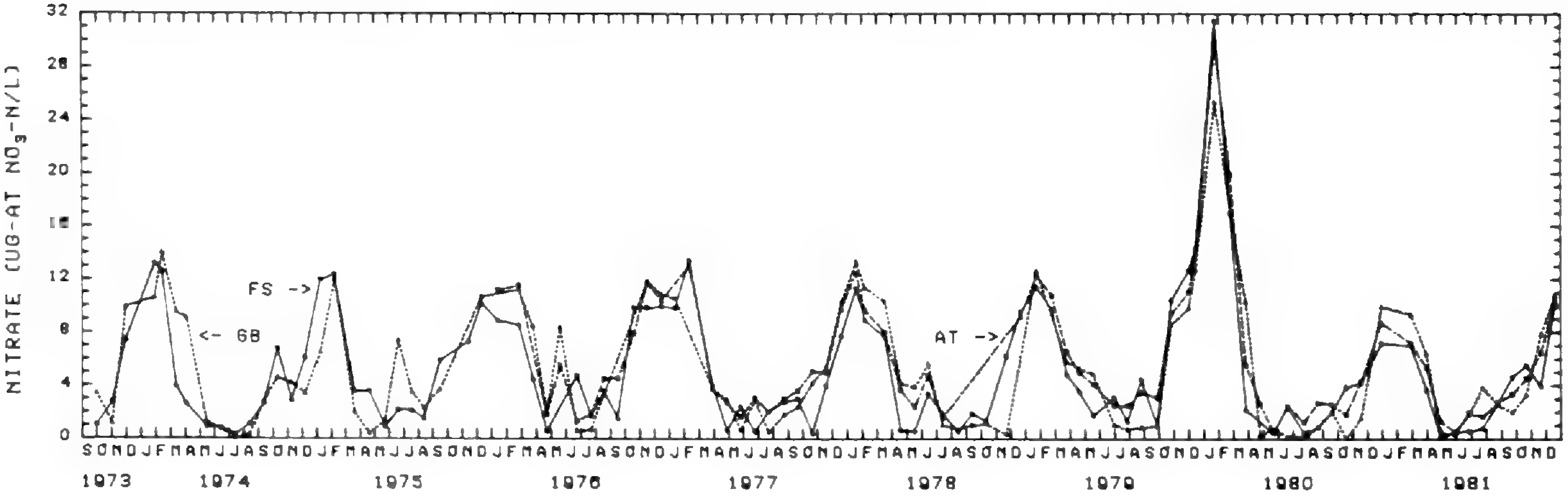

Figure 10. Seasonal variation of nitrogenous-nutrient levels (i.e. nitrate-N) on the nearshore open coast of New Hampshire (Jaffrey Point, Fort Stark) and within the Great Bay Estuary System (Atlantic Terminal and Great Bay) during 1973–1981 (based upon Emerich Penniman et al., 1985).

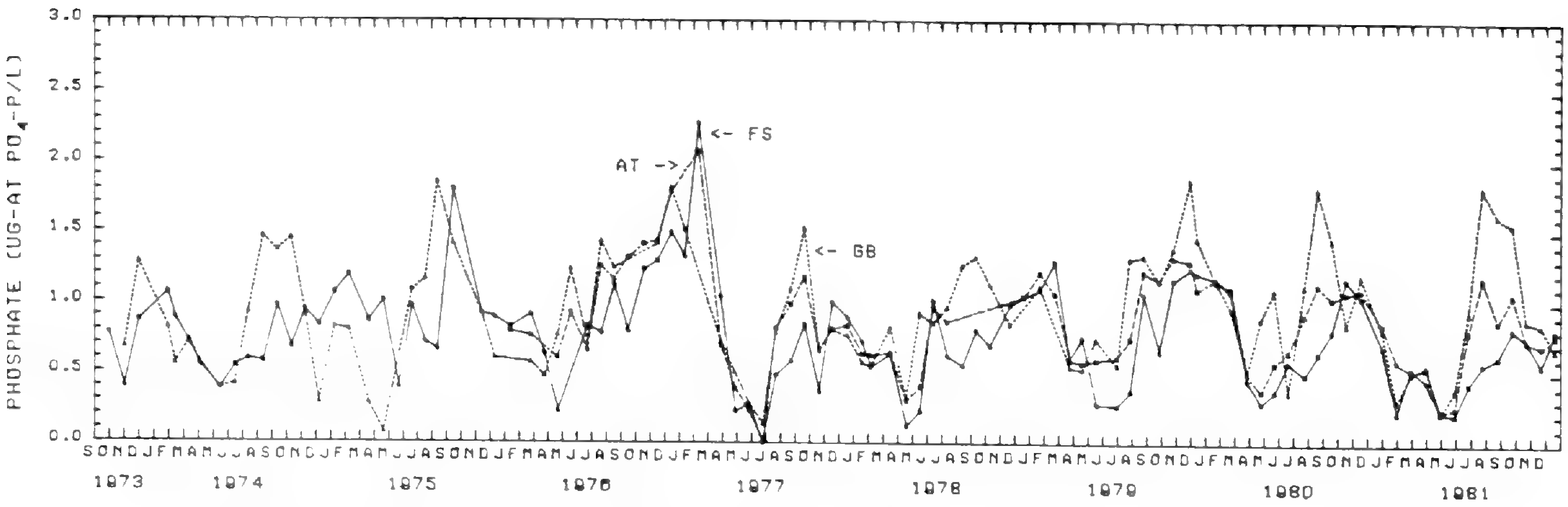

Figure 11. Seasonal variation of phosphorous-nutrient levels (i.e. orthophosphate-P) on the open coast of New Hampshire (Jaffrey Point, Fort Stark) and within the Great Bay Estuary System (Atlantic Terminal and Great Bay) during 1973–1981 (based upon Emerich Penniman et al., 1985).

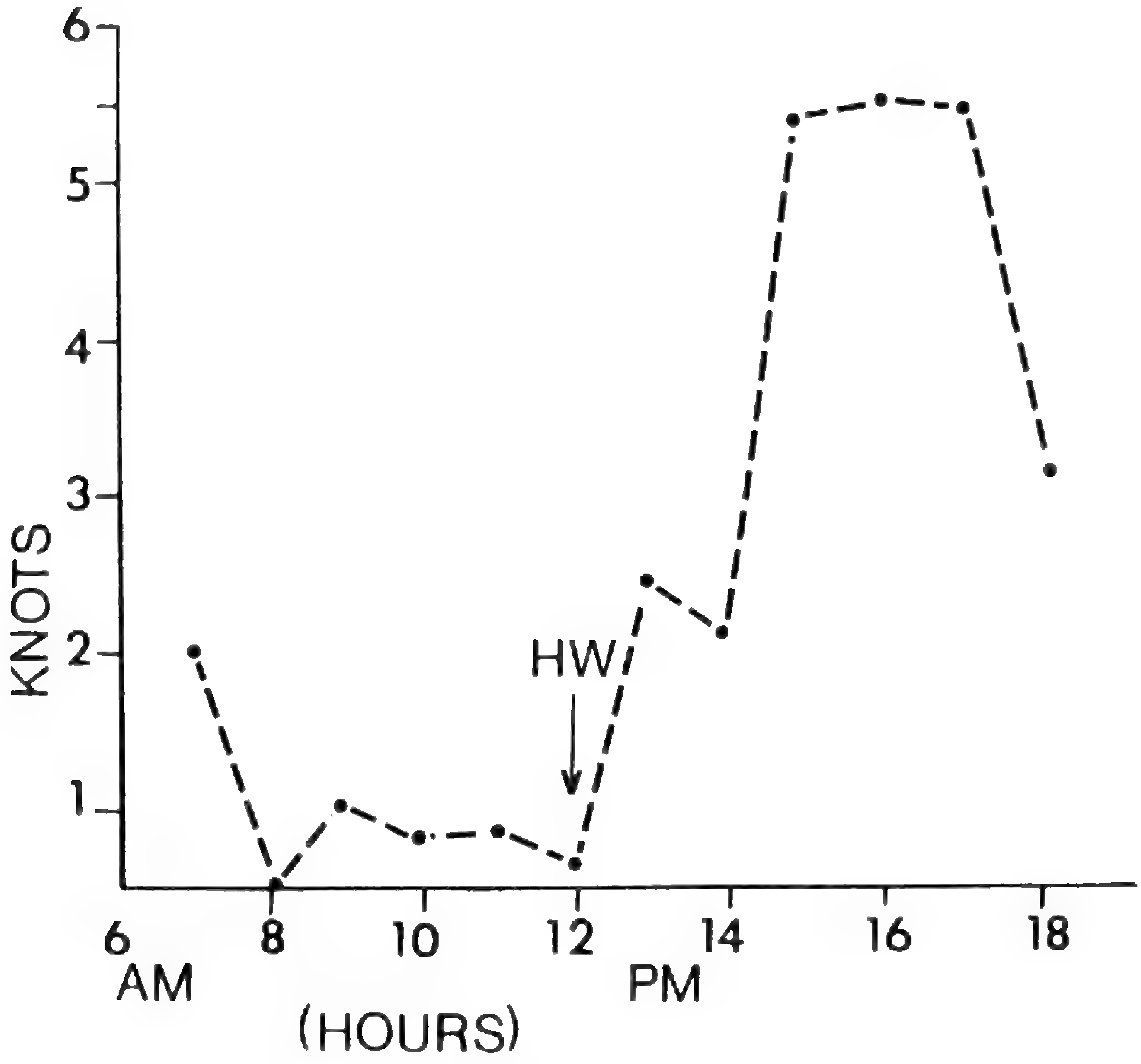

Figure 12. Diurnal variations of tidal currents at Dover Point.

SPECIES COMPOSITION

A total of 216 taxa is recorded from the coastal and estuarine environments of New Hampshire (Figures 1-5), including 58 Chlorophyceae, 66 Phaeophyceae and 92 Rhodophyceae (Tables I-III). Two of these 216 taxa (*Hecatonema terminalis* and *Myrionema magnusii*) were not collected by us, but they were recorded by Collins (1900) from the state with no specific dates nor collection sites. All of the other taxa, except for *Acrochaete repens, Bolbocoleon piliferum, Prasinocladus marinus* and *Sphaerotrichia divaricata,* which were only obtained in culture after their grow-out in enriched sea water media (Zechman and Mathieson, 1985), were collected in one or more estuarine and/or open coastal habitats. Eight of the 216 taxa recorded herein are new records for the state, including one brown (*Sphaerotrichia divaricata*) and seven red algae (*Audouinella violaceae, Callocolax neglectus, Ceramium elegans, Cruoriopsis ensis, Halosacciocolax kjellmanii, "Porphyrodiscus simulans"* and *Turnerella pennyi*). [*Porphyrodiscus simulans* and its other life history stages (cf. Farnham and Fletcher, 1976) are hereafter designated by quotes.] Each of the seven red algae represents either a range extension or a new record for the northeastern coast of North America. For example, the "fresh water" red alga *Audouinella violacea* is newly recorded from coastal waters of the northeast; it grows as an epiphyte on the fresh water red alga *Sacheria fucina,* and it may occur abundantly within riverine habitats. The specific parasite *Callocolax neglectus* which grows abundantly on *Callophyllis cristata,* was previously recorded from Greenland (Pedersen, 1976) and Newfoundland (South and Hooper, 1980). *Ceramium elegans* was earlier known from the Canadian Maritime Provinces (South, 1984; Taylor, 1957), while *Halosacciocolax kjellmanii* and *"Porphyrodiscus simulans"* were recorded from Newfoundland and the Canadian Maritime Provinces (South, 1984). The geographical distribution of *Turnerella pennyi* was previously recorded from the Arctic to the Atlantic coast of Nova Scotia, while Taylor (1957) only listed *"Cruoriopsis ensis"* from southern Massachusetts. The green alga *Codium fragile* ssp. *tomentosoides* has recently (1983) been found attached at Appledore Island, Maine, Isles of Shoals (Figure 2), and it could extend to adjacent New Hampshire sites (Carlton and Scanlon, 1985; Mathieson and Penniman, 1986a).

PHENOLOGY AND LONGEVITY

A summary of the temporal variation of seaweed taxa within estuarine-coastal waters of New Hampshire is given in Figure 13, based upon the data in Tables I–III. The number of taxa/month was highest in August (178) and lowest in January (105). Each of the three major groups of seaweeds showed a similar seasonal pattern, except that the Chlorophyceae had their highest number of taxa in July (42). Similar phenological patterns with summer maxima and winter minima have been noted in several other North Atlantic areas (Coleman and Mathieson, 1975; Lamb and Zimmerman, 1964; MacFarlane and Bell, 1933; Reynolds and Mathieson, 1975; Sears and Wilce, 1975). Chapman (1964) and Williams (1948, 1949) have emphasized that seasonally dynamic floras and a wide range of

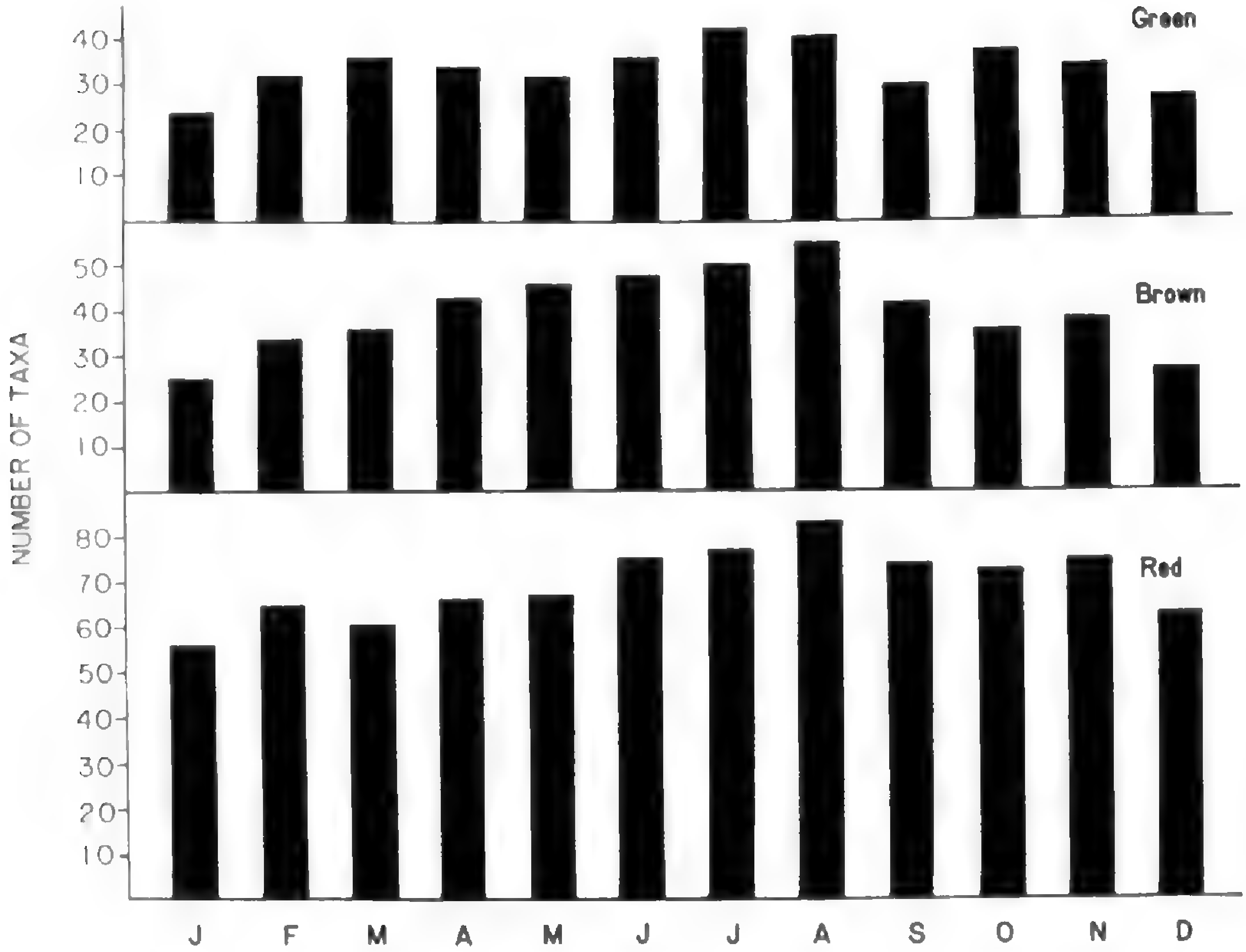

Figure 13. Temporal variations of seaweed taxa within estuarine-coastal waters of New Hampshire, expressed as the number of taxa/month.

annuals exist in areas with pronounced temperature fluctuations. The functional role of annuals in mediating the seasonal cycle of New Hampshire seaweeds is shown in Tables I–III.

Of the total algal flora outlined in Tables I–III, 113 taxa (52.3%) were designated as annuals and 100 taxa (46.3%) were interpreted as perennials (Figure 14). Three algae (*Cladophora sericea, Derbesia marina* and *Ulva lactuca*) or 1.4% of the flora, require further study as they may be either aseasonal annuals or pseudoperennials (*sensu* Knight and Parke, 1931). As outlined below, the longevity patterns (ratios of annuals/perennials and the percentage of perennial taxa) for the three major groups of seaweeds are conspicuously different:

1. Rhodophyceae 30 annuals/62 perennials (0.48:1) or 67.4% perennials
2. Phaeophyceae—36 annuals/30 perennials (1.2:1) or 45.5% perennials
3. Chlorophyceae—47 annuals/8 perennials (5.9:1) or 13.8% perennials

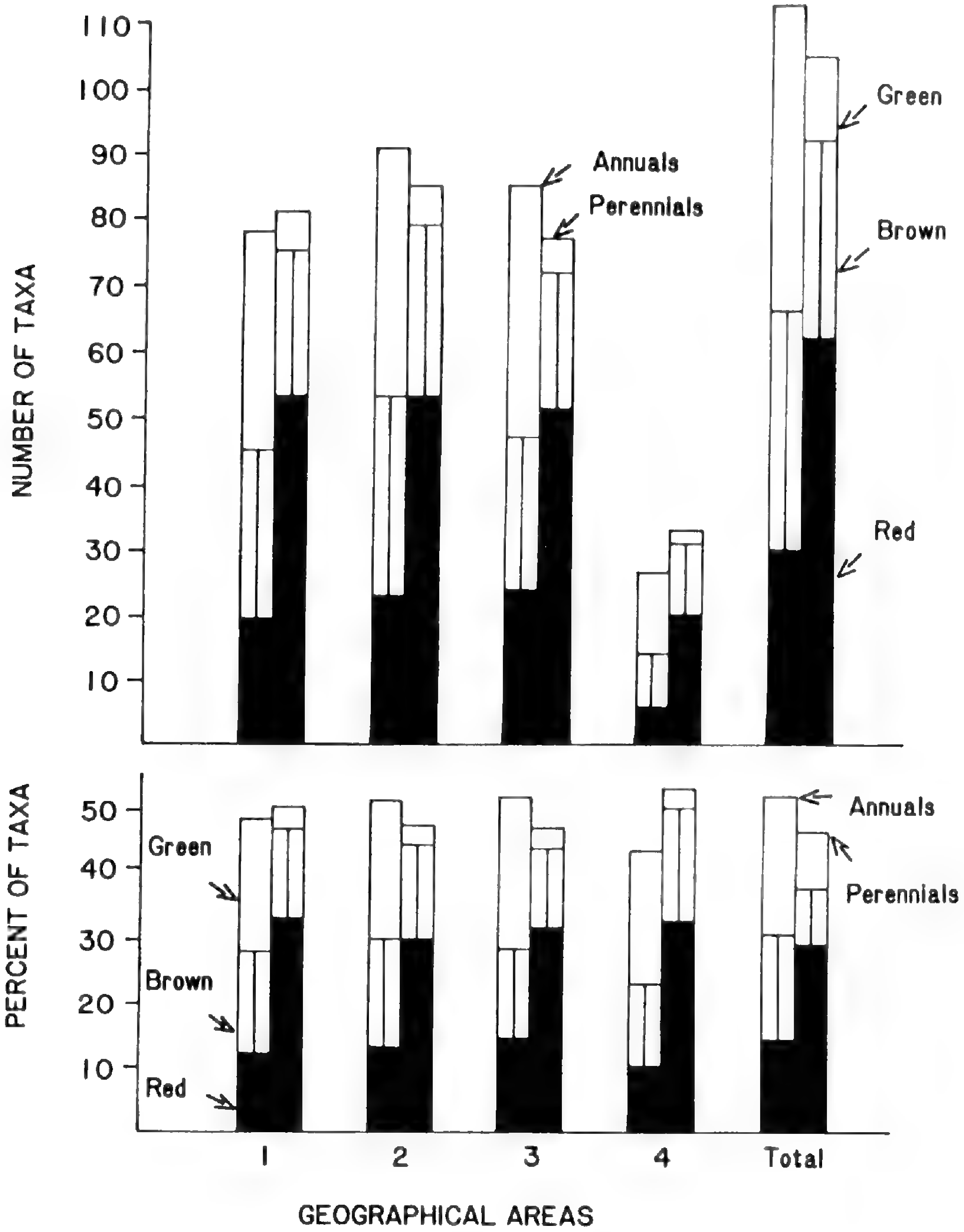

Figure 14. The number and percentage of annual and perennial chlorophycean, phaeophycean and rhodophycean taxa within estuarine-coastal waters of New Hampshire.

Thus, the red algae exhibit the greatest dominance by perennials, the brown algae have an intermediate pattern and the green algae exhibit the greatest dominance by annuals.

As outlined in Tables I–III, three distinct types of seasonal annuals (winter, spring and summer) plus aseasonal annuals can be distinguished, according to their season of maximum growth and development. No fall annuals were found, although many summer plants persist into fall and early winter. Thus, the fall season appears to be a transition period between summer and winter floras. Most of the seasonal annuals reproduce during their periods of maximum abundance. On the other hand some aseasonal annuals (*Petalonia fascia* and *Scytosiphon lomentaria* var. *lomentaria*) are reproductive throughout the year while others such as *Dumontia contorta* only reproduce during more restricted periods (Hehre and Mathieson, 1970; Kilar and Mathieson, 1978; Mathieson and Hehre, 1982, 1983). Similarly, these authors as well as Tveter-Gallagher et al. (1980), pointed out that many perennials are reproductive throughout the year, while others exhibit distinct reproductive periods.

Several taxa were only collected *in situ* a few times (*Chlorochytrium moorei, "Halicystis ovalis," Pringsheimiella scutata, Spirogyra* sp., *Stichococcus marinus, Stigeoclonium* sp., *Cladostephus spongiosus* forma *verticillatus, Eudesme virescens, Giffordia secunda, Scytosiphon lomentaria* var. *complanatus, Sorocarpus micromorus, Sphacelaria fusca, Audouinella polyides, Ceramium elegans, Colaconema polyides, "Cruoriopsis ensis," Erythropeltis discigera* var. *discigera, Halosacciocolax kjellmanii, "Porphyrodiscus simulans,"* and *Turnerella pennyi*). Several of these plants plus *Acrochaete repens, Bolbocoleon piliferum, Prasinocladus marinus* and *Sphaerotrichia divaricata,* which were only found in culture (Tables I–III), may have been missed due to their small stature. In contrast to these "rare" taxa, many of the larger perennial forms were ubiquitous at a wide variety of coastal and estuarine sites throughout the year. Specific details on the seasonal occurrence and longevity of each taxon are summarized in Tables I–III.

PATTERNS OF LOCAL DISTRIBUTION

A summary of the local distribution of the chlorophycean, phaeophycean and rhodophycean taxa in the four major coastal-estuarine areas in New Hampshire is shown in Figure 15. The highest number of taxa (179) was recorded from the nearshore open coast between Portsmouth and Seabrook. The species richness at the Isles of Shoals and within the Great Bay Estuary System was

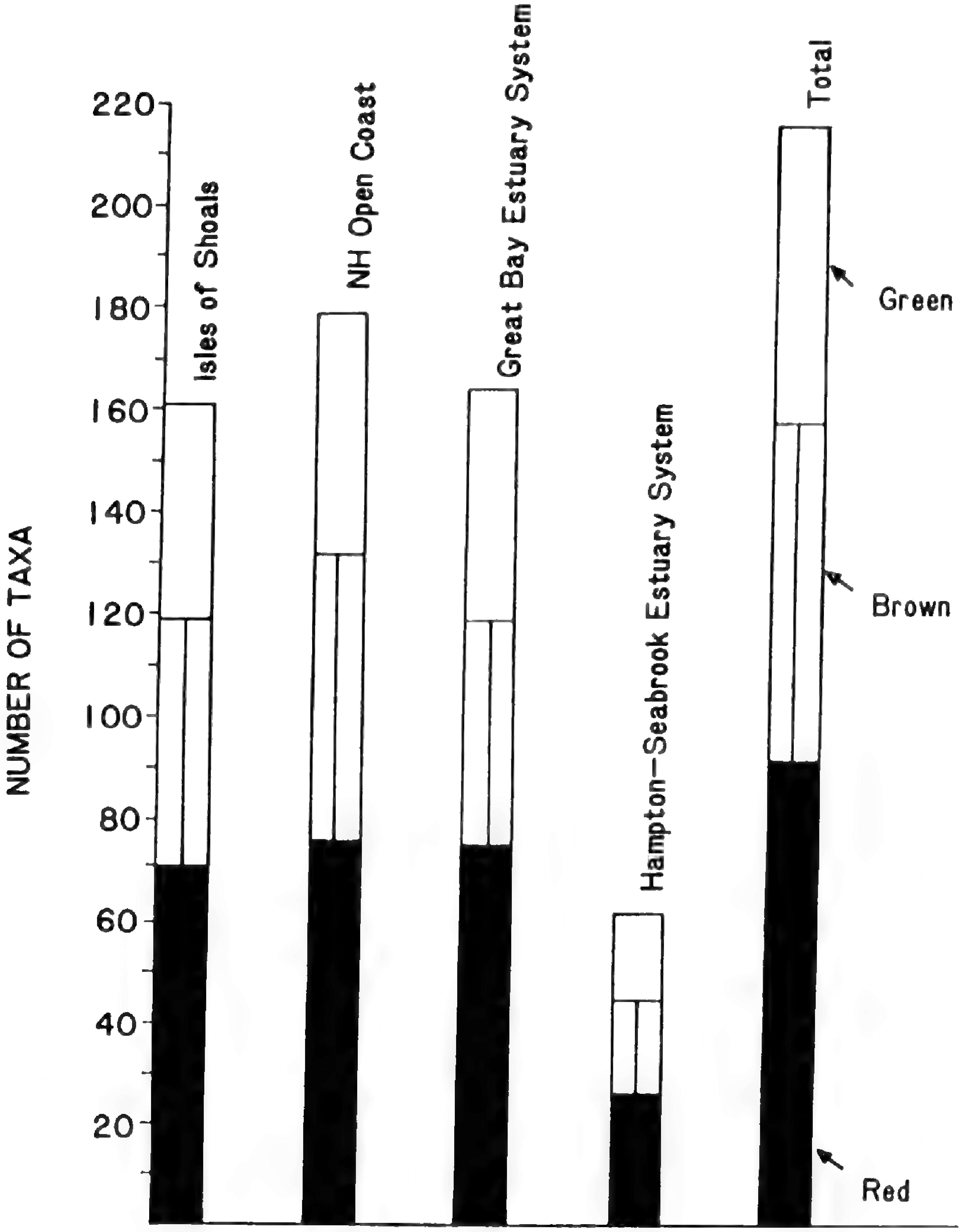

Figure 15. Local distribution of chlorophycean, phaeophycean and rhodophycean taxa within the four major coastal-estuarine areas in New Hampshire.

nearly the same (161 and 164 taxa, respectively), although the species composition of each was conspicuously different. The low species richness (63 taxa) within the Hampton-Seabrook Estuary System contrasts strongly with that of the Great Bay Estuary. Each of the three major groups of seaweeds exhibited their minimum number of species within the Hampton-Seabrook Estuary System. The Chloropyceae and Rhodophyceae had an approximate equality of species numbers at the two open coastal areas and within the Great Bay Estuary System, with 42–47 green algal taxa at the three habitats versus 71–76 red algae at the same three sites. In contrast, the Phaeophyceae exhibited a more pronounced difference between the nearshore open coast and the Great Bay Estuary System, with 56 taxa at the former and 44 taxa at the latter.

As noted by Mathieson and Fralick (1972), the low species richness within the Hampton-Seabrook Estuary may be associated with its limited acreage (reduced habitats) and lack of stable substrata. On the other hand, the relatively high species diversity at the Isles of Shoals (comparable to the nearshore open coast and the entire Great Bay Estuary System), is impressive as they are a small albeit relatively "pristine" set of islands (Mathieson and Penniman, 1986a).

The species composition within the Great Bay Estuary System is very different than that at the Shoals and the nearshore open coast, because of the presence of several freshwater algae, the enhanced number of "estuarine" taxa and the reduced number of "coastal" species. A similar reduction of open coastal species within estuarine habitats has been related to variable hydrographic conditions and limited rocky substrata (Doty and Newhouse, 1954; Hardwick-Witman and Mathieson, 1983; Mathieson and Fralick, 1972; Mathieson, Reynolds and Hehre, 1981).

The coastal and/or estuarine distributional patterns of each chlorophycean, phaeophycean and rhodophycean taxon are summarized in Tables I–III, as well as within the individual distribution maps (Figures 16–229). Overall, three basic patterns are evident as follows:

1. coastal—restricted to the open coast
2. cosmopolitan—present in both estuarine and open coastal environments
3. estuarine—restricted to estuarine environments

Approximately 23% of the total flora (49 of 216 taxa) were restricted to the open coast. Twenty-five of these taxa occurred in both open coastal habitats (Figures: 30. *Cladophora rupestris;* 33. *"Codiolum petrocelidis";* 36. *Derbesia marina;* 45. *Entocladia flus-*

trae; 47. *Gomontia polyrhiza;* 75. *Alaria esculenta;* 76. *Ascocyclus distromaticus;* 79. *Asperococcus fistulosus;* 106. *Laminariocolax tomentosoides;* 107. *Leathesia difformis;* 108. *Mikrosyphar porphyrae;* 115. *Protectocarpus speciosus;* 118. *Punctaria plantaginea;* 123. *Saccorhiza dermatodea;* 141. *Audouinella alariae;* 158. *Ceratocolax hartzii;* 168. *Devaleraea ramentaceum;* 170. *Erythropeltis discigera* var. *discigera;* 179. *Harveyella mirabilis;* 181. *Leptophytum foecundum;* 189. *Nemalion helminthoides;* 196. *Phyllophora traillii;* 200. *Phymatolithon rugulosum;* 210. *Polysiphonia novae-angliae;* 227. *Spermothamnion repens*). On the other hand, nine taxa were restricted to the Isles of Shoals (Figures: 25. *Chaetomorpha minima;* 35. *Codium fragile* subsp. *tomentosoides;* 58. *Pringsheimiella scutata;* 65. *Stichococcus marinus;* 83. *Cladostephus spongiosus* forma *verticillatus;* 93. *Fucus distichus* subsp. *anceps;* 130. *Sphacelaria fusca;* 178. *Halosacciocolax kjellmanii;* 191. *Pantoneura baeri*), while 13 were only collected from the nearshore open coast (Figures: 18. *Bolbocoleon piliferum;* 27. *Chlorochytrium moorei;* 48. *"Halicystis ovalis";* 56. *Prasinocladus marinus;* 92. *Eudesme virescens;* 101. *Giffordia secunda;* 128. *Sphacelaria arctica;* 131. *S. plumigera;* 132. *S. plumosa;* 134. *Sphaerotrichia divaricata;* 143. *Audouinella polyides;* 218. *Porphyropsis coccinea;* 229. *Turnerella pennyi*).

In contrast to the moderate number of open coastal taxa, 145 species or 67% of the total flora exhibited a cosmopolitan distribution, occurring in both open coastal and estuarine habitats. Several of these cosmopolitan species were broadly distributed in estuarine habitats (Figures: 17. *Blidingia minima;* 23. *Chaetomorpha linum;* 31. *Cladophora sericea;* 37, 38, 40, 41, 42 & 43. *Enteromorpha* ssp.; 51. *Monostroma grevillei;* 55. *Percursaria percursa;* 60. *Rhizoclonium riparium;* 67. *Ulothrix flacca;* 69. *Ulva lactuca;* 70. *Ulvaria obscura;* 77. *Ascophyllum nodosum;* 90. *Ectocarpus siliculosus;* 96. *Fucus distichus* subsp. *evanescens;* 98. *F. vesiculosus;* 111. *Petalonia fascia;* 114. *Pilayella littoralis;* 122. *Ralfsia verrucosa;* 125. *Scytosiphon lomentaria* var. *lomentaria;* 138. *Ahnfeltia plicata;* 151. *Callithamnion tetragonum;* 156. *Ceramium rubrum;* 160. *Chondrus crispus;* 165. *Cystoclonium purpureum;* 169. *Dumontia contorta;* 177. *Gymnogongrus crenulatus;* 180. *Hildenbrandia rubra;* 195. *Phyllophora pseudoceranoides;* 197. *P. truncata;* 202. *Polyides rotundus;* 205. *Polysiphonia flexicaulis;* 206. *P. harveyi;* 208. *P. nigra;* 209. *P. nigrescens;* 216. *Porphyra umbilicalis*). Many other cosmopolitan species were restricted to outer estuarine sites, that is, adjacent to the open coast, or they occurred as "disjunct" populations within estuarine tidal rapid sites such as Dover Point and Fox Point (Figures: 21. *Chaetomorpha aerea;* 24. *C. melagonium;* 34. *"Codiolum pusillum";* 52. *Monostroma pulchrum;* 57. *Prasiola stipitata;* 59. *Pseudendoclonium submarinum;* 73. *Urospora wormskioldii;* 74. *Agarum cribrosum;* 80. *Chorda filum;* 81. *C. tomentosa;* 85. *Desmarestia aculeata;* 86. *D. viridis;* 87. *Desmotrichum undulatum;* 88. *Dictyosiphon foeniculaceus;* 89. *Ectocarpus fasciculatus;* 91. *Elachista fucicola;* 94. *Fucus distichus* subsp. *distichus;* 95. *F. distichus* subsp. *edentatus;* 103. *Laminaria digitata;* 104. *L. longicruris;* 109. *Myrionema corunnae;* 112. *Petalonia zosterifolia;* 121. *Ralfsia fungiformis;* 135. *Spongonema tomentosum;* 137. *Ulonema rhizophorum;* 144. *Audouinella purpurea;* 152. *Callocolax neglectus;* 153. *Callophyllis cristata;* 161. *Choreocolax polysiphoniae;* 163. *Corallina officinalis;* 167. *Dermatolithon pustulatum;* 173. *Gigartina stellata;* 174. *Gloiosiphonia capillaris;* 182. *Leptophytum laeve;* 183. *Lithophyllum corallinae;* 184. *Lithothamnion glaciale;* 187. *Lomentaria orcadensis;* 188. *Membranoptera alata;* 192. *"Petrocelis cruenta";* 194. *Phycodrys rubens;* 198. *Phymatolithon laevigatum;* 199. *P. lenormandii;* 201. *Plumaria elegans;* 207. *Polysiphonia lanosa;* 212. *P. urceolata;* 213. *Porphyra leucosticta;* 220. *Ptilota serrata;* 221. *Rhodomela confervoides;* 222. *Rhodophyllis dichotoma;* 228. *"Trailliella intricata"*). A few cosmopolitan taxa were uncommon/rare on the open coast but widely distributed in estuarine habitats (Figures: 19. *Bryopsis plumosa;* 20. *Capsosiphon fulvescens;* 44. *Enteromorpha torta;* 49. *Kornmannia leptoderma;* 50. *Microspora pachyderma;* 71. *Ulvaria oxyspermum;* 139. *Antithamnion cruciatum;* 157. *Ceramium strictum;* 159. *Chondria baileyana;* 175. *Goniotrichum alsidii;* 186. *Lomentaria clavellosa* (only collected once on the open coast at Boone Island, Maine); 204. *Polysiphonia elongata*).

Sixteen seaweeds or 7% of the total flora were restricted to the Great Bay and/or Hampton-Seabrook Estuary Systems (Figures: 29. *Cladophora pygmaea;* 39. *Enteromorpha flexuosa* subsp. *flexuosa;* 78. *Ascophyllum nodosum* ecad. *scorpioides;* 117. *Punctaria latifolia;* 124. *Scytosiphon lomentaria* var. *complanatus;* 127. *Sorocarpus micromorus;* 136. *Stictyosiphon griffithsianus;* 149. *Callithamnion byssoides;* 155. *Ceramium elegans;* 166. *Dasya baillouvi-*

ana; 176. *Gracilaria tikvahiae;* 185. *Lomentaria baileyana;* 203. *Polysiphonia denudata;* 211. *P. subtilissima;* 217. "*Porphyrodiscus simulans*"; 224. *Rhodophysema georgii*). Six "fresh-water" taxa were found attached in riverine habitats near the headwaters of tidal tributaries (Figures: 53. *Mougeotia* sp.; 54. *Oedogonium* sp.; 62. *Spirogyra* sp.; 66. *Stigeoclonium* sp.; 146. *Audouinella violacea;* 225. *Sacheria fucina*). Some of the latter species, such as *Sacheria fucina,* are known to be tolerant of reduced salinities (Wood and Straughan, 1953).

As outlined by Mathieson, Reynolds and Hehre (1981), closely related taxa often have distinct distributional patterns within estuaries. The different taxa of *Chaetomorpha* (Figures 21–26), *Cladophora* (Figures 28–31), *Monostroma* (Figures 51, 52), *Rhizoclonium* (Figures 60, 61), *Ulvaria* (Figures 70, 71), *Ectocarpus* (Figures 89, 90), *Fucus* (Figures 93–98), *Laminaria* (Figures 103–105), *Punctaria* (Figures 117, 118), *Ralfsia* (Figures 119–122), *Sphacelaria* (Figures 128–133), *Audouinella* (Figures 141–146), *Callithamnion* (Figures 149–151), *Ceramium* (Figures 154–157), *Lomentaria* (Figures 185–187), *Phyllophora* (Figures 195–197), *Phymatolithon* (Figures 198–200), *Polysiphonia* (Figures 203–212) and *Porphyra* (Figures 213–216) can all be cited. For example, of the six *Chaetomorpha* species recorded (Table I, Figures 21–26), one (*C. minima*) was restricted to the Isles of Shoals, while five (*C. aerea, C. brachygona, C. linum, C. melagonium* and *C. picquotiana*) exhibited cosmopolitan distributional patterns of varying degrees. Overall, *C. linum* was the most ubiquitous and broadly distributed species (Figure 23). The different taxa of *Fucus* exhibited a similar pattern (Tables I and II, Figures 93–98), with one taxon (*F. distichus* subsp. *anceps*) being restricted to the Isles of Shoals, and five (*F. distichus* subsp. *distichus, F.d.* subsp. *edentatus, F.d.* subsp. *evanescens, F. spiralis* and *F. vesiculosus*) exhibiting varying cosmopolitan distributional patterns. *Fucus vesiculosus* was the most broadly distributed taxon of this group (Figure 98). A comparison of the ten *Polysiphonia* species (Table III, Figures 203–212) shows that two species (*P. denudata* and *P. subtilissima*) were restricted to estuarine environments, one (*P. elongata*) was rare on the open coast, six (*P. flexicaulis, P. harveyi, P. lanosa, P. nigra, P. nigrescens* and *P. urceolata*) exhibited cosmopolitan distributions, and one (*P. novae-angliae*) was restricted to the open coast. Similar distributional comparisons can also be made for different genera in the same families (*sensu* Smith, 1950; South, 1984): Ulotrichaceae (*Stichococcus* and *Ulothrix,* Figures 65, 67 and 68); Chaetophoraceae (*Acrochaete, Bolbocoleon, Entocladia, Pringsheimiella, Pseudendoclonium* and *Stigeoclonium,* Figures 16, 18, 45, 46, 58, 59 and 66); Acrosiphoniaceae (*Spongomorpha* and *Urospora,* Figures 63, 64, 72 and 73); Percursariaceae (*Blidingia, Gomontia, Kornmannia, Monostroma* and *Percursaria,* Figures 17, 47, 49, 51, 52 and 55); Ulvaceae (*Capsosiphon, Enteromorpha, Ulva* and *Ulvaria,* Figures 20, 37–44, 69, 70 and 71); Cladophoraceae (*Chaetomorpha, Cladophora* and *Rhizoclonium,* Figures 21–26, 28–31, 60 and 61); Bryopsidaceae (*Bryopsis* and *Derbesia,* Figures 19 and 36); Zygnemataceae (*Mougeotia* and *Spirogyra,* Figures 53 and 62); Ectocarpaceae (*Ectocarpus, Giffordia, Laminariocolax, Mikrosyphar, Pilayella, Sorocarpus* and *Spongonema,* Figures 89, 90, 99–101, 106, 108, 114, 127 and 135); Ralfsiaceae (*Petroderma, Pseudolithoderma, Ralfsia fungiformis, R. verrucosa* and *Sorapion,* Figures 113, 116, 121, 122 and 126); Myrionemataceae (*Ascocyclus, Myrionema, Protectocarpus* and *Ulonema,* Figures 76, 109, 110, 115 and 137); Chordariaceae (*Chordaria, Eudesme* and *Sphaerotrichia,* Figures 82, 92 and 134); Striariaceae (*Isthmoplea* and *Stictyosiphon,* Figures 102 and 136); Punctariaceae (*Asperococcus, Desmotrichum* and *Punctaria,* Figures 79, 87, 117 and 118); Scytosiphonaceae (*Petalonia* and *Scytosiphon,* Figures 111, 112, 124 and 125); Laminariaceae (*Agarum, Laminaria* and *Saccorhiza,* Figures 74, 103–105 and 123); Fucaceae (*Ascophyllum* and *Fucus,* Figures 77, 78 and 93–98); Cystocloniaceae (*Cystoclonium* and *Rhodophyllis,* Figures 165 and 222); Phyllophoraceae (*Ahnfeltia, Ceratocolax, Gymnogongrus* and *Phyllophora,* Figures 138, 158, 177 and 195–197); Gigartinaceae (*Chondrus* and *Gigartina,* Figures 160 and 173); Corallinaceae (*Clathromorphum, Corallina, Dermatolithon, Fosliella, Leptophytum, Lithophyllum, Lithothamnion* and *Phymatolithon,* Figures 162, 163, 167, 172, 181–184 and 198–200); Kallymeniaceae (*Callocolax* and *Callophyllis,* Figures 152 and 153); Choreocolaceae (*Choreocolax* and *Harveyella,* Figures 161, 179); Palmariaceae (*Devaleraea, Halosacciocolax, Palmaria* and *Rhodophysema,* Figures 168, 178, 190, 223 and 224); Ceramiaceae (*Antithamnion, Antithamnionella, Callithamnion, Ceramium, Plumaria, Pterothamnion, Ptilota, Scagelia* and *Spermothamnion,* Figures 139, 140, 149–151, 154–157, 201, 219, 220, 226 and 227);

Delesseriaceae (*Membranoptera, Pantoneura* and *Phycodrys,* Figures 188, 191 and 194); Rhodomelaceae (*Chondria, Polysiphonia* and *Rhodomela,* Figures 159, 203 212 and 221); Erythropeltidaceae (*Erythropeltis, Erythrotrichia* and *Porphyropsis,* Figures 170, 171 and 218); Bangiaceae (*Bangia* and *Porphyra,* Figures 147 and 213–216). The members of the Gigartinaceae can be cited as specific examples (Figures 160 and 173); both *Chondrus* and *Gigartina* exhibit cosmopolitan distribution patterns, although *G. stellata* has the most restricted outer estuarine pattern and a conspicuous reduction of stature in estuarine habitats (Burns and Mathieson, 1972b).

Based upon the data in Tables I III plus previous floristic studies (Hehre and Mathieson, 1970; Mathieson and Hehre, 1982, 1983), it is apparent that several endophytic, epiphytic and parasitic seaweeds and their respective "hosts" demonstrate contrasting distributional patterns. The following taxa can be cited as examples:

1. endophytic *Mikrosyphar porphyrae* growing in various *Porphyra* species, particularly *P. umbilicalis* (Figures 108, 213–216)
2. epiphytic *Ascocyclus distromaticus* growing on *Palmaria palmata* (Figures 76, 190); *Elachista fucicola* on *Ascophyllum nodosum* (Figures 77, 91); *Laminariocolax tomentosoides* and *Myrionema corunnae* on various *Laminaria* species (Figures 103–106, 109); *Protectocarpus speciosus* on *Chaetomorpha aerea* (Figures 21, 115); *Ulonema rhizophorum* on *Dumontia contorta* (Figures 137, 169); *Audouinella alariae* on *Alaria esculenta* (Figures 75, 141); and *A. violacea* on *Sacheria fucina* (Figures 146, 225)
3. parasitic *Callocolax neglectus* growing on *Callophyllis cristata* (Figures 152, 153); *Ceratocolax hartzii* on *Phyllophora truncata* (Figures 158, 197); *Choreocolax polysiphoniae* on *Polysiphonia lanosa* (Figures 161, 207); *Halosacciocolax kjellmani* on *Palmaria palmata* (Figures 178, 190); *Harveyella mirabilis* on *Rhodomela confervoides* (Figures 179, 221); and *Polysiphonia lanosa* on *Ascophyllum nodosum* (Figures 77, 207).

Polysiphonia lanosa (Figures 77, 207), *Laminariocolax tomentosoides* (Figures 103–106) and *Choreocolax polysiphoniae* (Figures 161, 207) are representative of the above-described species, except for *Audouinella alariae* (Figures 75, 141) and *A. violacea* (Figures 146, 225). That is, the hemiparasite *P. lanosa,* which grows abundantly on *A. nodosum* on the open coast, is restricted to outer estuarine sites, even though its host is abundant and widely distributed (Fralick and Mathieson, 1975). The common epiphyte *L. tomentosoides* and the specific parasite *C. polysiphoniae* show a similar restricted estuarine distribution versus their hosts. *Audouinella alariae* and *A. violacea* were the only species with approximately the same distribution patterns as their hosts *Alaria esculenta* and *Sacheria fucina,* respectively.

As noted by Dixon (1965), a comparison of the distributional patterns of life history stages of individual taxa can be quite informative. Deviations from a "theoretical" life history can occur geographically due to perennation and various selective mechanisms operating against a particular genome (Mathieson and Burns, 1975; Mathieson and Norall, 1975a, b; Norall et al., 1981). Dixon (1965) described the example of gametophytic *Asparagopsis armata* and tetrasporic *Falkenbergia rufolanosa,* which may exhibit independent vegetative propagation and deviations from their "theoretical" life histories at northern latitudes. The recently recorded differences in geographical distribution in Europe for the two phases (Conway, 1960; Thomas, 1955) may be a reflection of independent vegetative propagation. In comparing the coastal and/or estuarine distribution patterns of different life history phases of New England seaweeds (Tables I–III), several geographical contrasts are evident, perhaps due to the strong environmental gradient within these areas (see earlier description), the different physiological tolerances of various phases (Mathieson and Burns, 1975; Mathieson and Norall, 1975a, b; Norall et al., 1981), the different modes and magnitude of vegetative propagation, and other factors. For example, the "*Codiolum gregarium/pusillum*" sporophytic stages of *Urospora* and *Ulothrix* spp. (Kornmann and Sahling, 1977; Scagel, 1966; South, 1984) have a more localized estuarine distribution than their corresponding gametophytic phases (Figures 32, 34, 67, 72, 73). A similar trend is evident in Figures 33 and 64 for the endophytic "*Codiolum petrocelidis*" sporophyte of *Spongomorpha spinescens* (Jonsson, 1958; Scagel, 1966). Both gametophytic "*Halicystis ovalis*" and sporophytic *Derbesia marina* (Sears and Wilce, 1970) are restricted to the open coast, with the former being rare and the latter more common (Figures 36, 48). The crustose sporophytic "*Ralfsia bornetii/clavata*" and foliose gametophytic stages of *Petalonia fascia* (Edelstein et al.,

1970) both exhibit cosmopolitan distributional patterns, although the foliose stage is more widely distributed than the crustose phase (Figures 111, 119, 120). Similarly, the crustose tetrasporophyte "*Porphyrodiscus simulans*" of *Ahnfeltia plicata* (Farnham and Fletcher, 1976) was only found at one estuarine site, while the gametophytic phase was collected at diverse open coastal and estuarine habitats (Figures 138, 217). The sporophytic "*Trailliella intricata*" phase of *Bonnemaisonia hamifera* (Chihara, 1961, 1962), also exhibits a more localized distribution than its gametophytic phase (Figures 148, 228). Lastly, the crustose sporophytic "*Petrocelis cruenta*" and upright gametophytic phases of *Gigartina stellata* (Fletcher and Irvine, 1982; Guiry and Coleman, 1982; West and Polanshek, 1975; West et al., 1977) both extend from the open coast into the outer-mid portions of the Great Bay Estuary System (Figures 173, 192).

Several unique ecological or phenotypic patterns were also evident. For example, the perennial psammophytic "sand-loving" (Mathieson, 1982b) brown alga *Sphacelaria radicans* was restricted to a few sand-abraded open coastal (Daly and Mathieson, 1977) and sandy outer estuarine habitats (Figure 133). Further, attached populations of *Ascophyllum nodosum* were collected abundantly at diverse open coastal and estuarine sites (Figure 77), while the ecad *scorpioides* was restricted to sheltered estuarine sites (Figure 78), entangled amongst *Spartina alterniflora* (Chock and Mathieson, 1976). Two examples of phenotypic plasticity should also be noted. The fucoid brown alga *Fucus vesiculosus* primarily exhibits a spiraled morphology (var. *spiralis* in Taylor, 1957) in estuarine habitats, while the typical non-spiraled plant is most abundant in open coastal habitats, particularly exposed sites. Locally, most populations of *Cystoclonium purpureum* have tendril-like branches (var. *cirrhosum* in Taylor, 1957); even so, some estuarine plants exhibit radiating burr-like branches (forma *stellatum*, Collins, 1906b), which Taylor (1957) suggested are a pathological state. Although South (1984) and others suggested that subspecific taxa of *C. purpureum* are insufficiently distinct to warrant retention, the "stellatum-type" morphology seems to be restricted to sheltered estuarine sites.

In comparing the local distribution of plants based upon culture and *in situ* collections (Tables I–III), several interesting contrasts can be made. As noted earlier, four taxa were only recorded in culture (*Acrochaete repens, Bolbocoleon piliferum, Prasinocladus marinus* and *Sphaerotrichia divaricata,* Figures 16, 18, 56, 134), while the local distributional records of an additional four taxa ("*Codiolum pusillum,*" *Microspora pachyderma, Desmotrichum undulatum* and *Isthmoplea sphaerophora,* Figures 34, 50, 87, 102) were supplemented by culture information. Thus, the single estuarine record of "*C. pusillum*" was based upon culture findings, while similar statements can be made about the solitary nearshore open coastal records for *M. pachyderma, D. undulatum* and *I. sphaerophora.* Presumably these culture records are based upon the plants being rare in nature, cryptic in size, and juvenile and adult stages having different physiological tolerances/optima, or other factors. In this context, Mathieson and Hehre (1983) noted that attached populations of freshwater algae like *M. pachyderma* are typically restricted to inner estuarine/riverine habitats. Even so, juvenile (cultured) populations of *M. pachyderma* exhibit a wide tolerance to salinity, which suggests that other biological factors may restrict the plant's growth *in situ* (Zechman and Mathieson, 1985). Several unique culture records for *Enteromorpha compressa, Spongomorpha arcta, Ulvaria oxysperma, Urospora wormskioldii, Desmotrichum undulatum* and *Porphyropsis coccinea* should also be noted (Figures 38, 63, 71, 73, 87, 218). For example, the ubiquitous "estuarine" alga *U. oxysperma* was only found at four open coastal locations, one of which was based upon its presence in culture (Figure 71).

PHYSIOLOGICAL ECOLOGY AND DISTRIBUTIONAL PATTERNS OF SELECT SEAWEEDS

Several estuarine taxa, or seaweeds that are rare on the open coast of New Hampshire, represent disjunct populations north of Cape Cod, Massachusetts, on the northeast coast of North America: *Bryopsis plumosa* (Figure 19); *Ulvaria oxysperma* (Figure 71); *Antithamnion cruciatum* (Figure 139); *Ceramium strictum* (Figure 157); *Chondria baileyana* (Figure 159); *Dasya baillouviana* (Figure 166); *Gracilaria tikvahiae* (Figure 176); *Lomentaria baileyana* (Figure 185); *Polysiphonia denudata* (Figure 203); and *P. subtilissima* (Figure 211). These "southerly" taxa are more widely distributed south than north of Cape Cod and several of them extend to the tropics, Bermuda, Florida, etc. (Taylor, 1957, 1960). At their northern distributional limits, each of these plants occurs primarily in shallow embayments or protected habitats such as the Great Bay Estuary System or Northumberland Straits near Prince Edward Island, New Brunswick, Canada. All of these species, except for *G. tikvahiae*, are summer annuals (Tables I and III) at their northern limits, and they may have "modified" life histories (Mathieson and Burns, 1975; Norall et al., 1981) and extensive vegetative reproduction. As noted earlier, the hydrographic conditions within such northern latitudes are much more variable than within the central portion of the plant's geographical range. Thus, the phenologies of such "southerly" species are often conspicuously different in northern than in southern geographies (Hehre and Mathieson, 1970; Mathieson and Dawes, 1975).

Bousfield and Thomas (1975) have recorded similar disjunct patterns for many shallow water marine animals between Cape Cod, the northern Gulf of Maine and/or the Gulf of St. Lawrence. Many animal populations having similar temperature requirements are isolated from each other by hundreds of miles of climatically "unfavorable" marine coastlines, particularly during the reproductive period that is critical to natural dispersal and to maintenance of homogenous populations. The same authors speculated that the most satisfactory explanation of this distribution is an historical one; during a "hypsithermal" or warm period 7500–9500 years ago, the relatively shallow shelf waters between Cape Cod and the Gulf of St. Lawrence provided a uniform summer-warm environment and dispersal pathway. Subsequent drowning and deeping of the inshore coastal areas and increased upwelling in the Gulf of Maine during the past 5000 years have depressed the summer temperatures to present-day cool levels. In "post-hypsithermal" times the warm water fauna gradually disappeared from the cooling open coastal areas, and populations like those in the Gulf of St. Lawrence became regionally restricted and effectively isolated from the main populations in southern New England and further south. McAlice (1981) has given a similar explanation for the post-glacial history of the copepod *Acartia tonsa* in the Gulf of Maine and the Gulf of St. Lawrence. He suggested that the northern populations of this copepod, which occur in warm estuarine headwaters north of Cape Cod, are relict ones, derived from a distribution that was once continuous from Cape Cod to the Northumberland Strait (New Brunswick–Prince Edward Island). He further suggested that the disjunction of *A. tonsa* at its present refuges may make it useful for studies on rates of speciation.

The ideas presented by Bousfield and Thomsa (1975) and McAlice (1981) with respect to disjunct animal distributions would appear to be applicable to seaweeds as well. With the advent of cooling coastal waters, populations of some seaweeds may have been forced into warm estuarine habitats, while the main coastal populations receded southward. If, as McAlice (1981) suggested, these relict populations became reproductively isolated due to lower water temperatures and westerly currents, then the potential was established for genetic differentiation. The likelihood of this occurrence would be increased by differences in environmental conditions imposed upon the populations at their respective locations. Although northern estuaries provide warm summer temperatures required for the growth of "southerly" species, these estuarine populations must tolerate reduced and/or fluctuating salinities and extremely cold winter conditions. For example, the red alga *Polysiphonia subtilissima* is primarily restricted in New Hampshire–Maine to inner riverine habitats (Figure 211) where temperatures vary from 0–26° C, and salinities from 0–22 ‰ (Norall and Mathieson, 1976). Since *P. subtilissima* grows in northern locations as a pseudoperennial, regenerating from perennating holdfast filaments (Hehre and Mathieson, 1970; Yarish and Edwards, 1982), it must tolerate this entire range of conditions. South of Cape Cod, the same species may also occur on the open coast (Mathieson and Dawes, 1975) where it is exposed to more uniform temperatures and stable, coastal salinities. Consequently, broader temperature and salinity tolerances and lower optima would be of adaptive significance in northern disjunct seaweed populations, while the same attributes would be relatively unimportant to the continuous "southerly" coastal populations.

Fralick and Mathieson (1975) and Mathieson and Burns (1971), among others, have attempted to correlate the physiological ecology and estuarine distributional patterns of several seaweeds. For example, Fralick and Mathieson (1975) compared the photosynthesis and respiration of four species of *Polysiphonia* under different light, temperature and salinity conditions and found that they could be separated into a "cold water" group (*P. lanosa* and *P. elongata*) and a group with warm-water affinities (*P. nigrescens* and *P. subtilissima*). They speculated that the horizontal distribution of these four *Polysiphonia* taxa within the Great Bay Estuary System (Figure 204, 207, 209, 211) was primarily governed by their varying tolerances to high temperatures and low salinities. Thus, *P. subtilissima,* which had the highest temperature optimum, penetrated the furthest into the estuary (Figure 211), while *P. lanosa,* which had the lowest temperature optimum, was restricted to the more coastal stations (Figure 207). Mathieson and Burns (1971) conducted a similar physiological study of the closely-related gigartinaleanm red algae *Chondrus crispus* and *Gigartina stellata.* Both species exhibited broad tolderances to salinity. Even so, *C. crispus* showed its maximum photosynthesis and minimum respiration at 24 ‰, in agreement with the more open coastal habitat of *Gigartina* and the more estuarine habitat of *Chondrus* (Figures 160, 173). Culture studies of juvenile stages (sporelings from carpospores) from both plants have demonstrated a similar restricted tolerance to reduced salinities for *G. stellata* as compared to *C. crispus* (Burns and Mathieson, 1972a). The above-described physiological and culture studies, including those of Zechman and Mathieson (1985), demonstrate the potential for experimentally evaluating the distributional patterns of diverse seaweeds (Hoek, 1982a, b).

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Key to Tables I–III

x = present
* = obtained in culture
** = residual basal material

Longevity: Ann. = annual
AAnn. = aseasonal annual
Per. = perennial
PPer. = pseudoperennial

Local Distribution: 1 = Isles of Shoals
2 = Nearshore open coast between Portsmouth and Seabrook
3 = Hampton-Seabrook Estuary System
4 = Great Bay Estuary System

Table I: Seasonal occurrence, longevity and local distribution of Chlorophyceae

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Acrochaete repens N. Pringsh.			X*				X*						Ann.	2*, 4*
Blidingia minima (Näg. *ex* Kütz.) Kylin	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Bolbocoleon piliferum N. Pringsh.			X*				X*						Ann.	2*
Bryopsis plumosa (Huds.) C. Ag.		X**				X	X	X	X	X	X	X	Ann.	1–4
Capsosiphon fulvescens (C. Ag.) Setch. *et* Gardn.			X*		X	X	X	X	X	X	X	X	Ann.	2, 4
Chaetomorpha aerea (Dillw.) Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Chaetomorpha brachygona Harv.	X		X		X	X	X	X	X	X	X	X	Ann. (?)	1, 2, 4
Chaetomorpha linum (O. F. Müll.) Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Chaetomorpha melagonium (Web. *et* Mohr) Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Chaetomorpha minima Collins F. *et* Herv.										X	X		Ann. (?)	1
Chaetomorpha picquotiana Mont. *ex.* Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Chlorochytrium moorei Gardn.										X			Ann.	2
Cladophora albida (Huds.) Kütz.		X	X	X		X	X	X		X		X	AAnn.	1, 2, 4
Cladophora pygmeaea Reinke	X	X	X	X	X	X	X	X	X	X			Per.	4
Cladophora rupestris (L.) Kütz.		X				X		X		X			Per.	1, 2
Cladophora sericea (Hud.) Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	AAnn. or PPer.	1–4
"*Codiolum gregarium* A. Braun"							X*	X			X		Ann.	2, 4

Table I: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
"*Codiolum petrocelidis* Kuck."			X					X					Ann. (?)	1, 2
"*Codiolum pusillum* (Lyngb.) Kjellm."		X				X	X	X	X	X	X	X	Ann.	1, 2, 4*
Codium fragile (Sur.) Hariot subsp. *tomentosoides* (van Goor) Silva				X	X			X					Per.	1
Derbesia marina (Lyngb.) Solier				X	X						X		Ann. or PPer.	1, 2
Enteromorpha clathrata (Roth) Grev.				X		X	X	X	X	X	X	X	Ann.	1–4
Enteromorpha compressa (L.) Grev.	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Enteromorpha flexuosa (Wulf. *ex* Roth) J. Ag. subsp. *flexuosa* Bliding							X		X	X			Ann.	4
Enteromorpha flexuosa (Wulf. *ex* Roth) J. Ag. subsp. *paradoxa* (Dillw.) Bliding		X		X			X	X	X	X	X	X	Ann.	1–4
Enteromorpha intestinalis (L.) Link	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Enteromorpha linza (L.) J. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Enteromorpha prolifera (O. F. Müll.) J. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Enteromorpha torta (Mert. *in* Jürg.) Reinb.				X			X	X	X	X		X	Ann.	2, 4
Entocladia flustrae (Reinke) Batt.		X		X		X							Ann. (?)	1, 2
Entocladia viridis Reinke	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1, 2, 4
Gomontia polyrhiza (Lagerh.) Bornet *et* Flah.			X					X					Ann. (?)	1, 2

Table I: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
"*Halicystis ovalis* (Lyngb.) Aresch."							X						Per. (?)	2
Kornmannia leptoderma (Kjellm.) Bliding					X	X	X	X	X				Ann.	2, 4
Microspora pachyderma (Wille) Lagerh.	X	X	X	X	X	X*	X*			X	X*		Ann.	2*, 4
Monostroma grevillei (Thur.) Wittr.	X	X	X	X	X	X				X	X	X	Ann.	1–4
Monostroma pulchrum Farl.			X	X	X	X							Ann.	1, 2, 4
Mougeotia sp.							X						Ann.	4
Oedogonium sp.								X	X				Ann.	4
Percursaria percursa (C. Ag.) Rosenv.		X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Prasinocladus marinus (Cienk.) Waern							X*						Ann.	2*
Prasiola stipitata Suhr. *in* Jessen	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1, 2, 4
Pringsheimiella scutata (Reinke) Marchew.			X							X			Ann. (?)	1
Pseudendoclonium submarinum Wille							X	X			X		AAnn.	1, 4
Rhizoclonium riparium (Roth) Harv.	X	X	X	X	X	X	X	X	X	X	X		AAnn.	1–4
Rhizoclonium tortuosum (Dillw.) Kütz.	X	X	X	X	X	X	X	X	X	X	X		AAnn. (?)	1, 2, 4
Spirogyra sp.							X						Ann.	4
Spongomorpha arcta (Dillw.) Kütz.		X	X	X	X	X	X	X	X	X	X	X	Ann.	1, 2, 4
Spongomorpha spinescens Kütz.				X	X	X	X	X		X	X	X	Ann.	1, 2, 4
Stichococcus marinus (Wille) Hazen						X							Ann.	1

Table I: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Stigeoclonium sp.			X										Ann.	4
Ulothrix flacca (Dillw.) Thur. *in* Le Jolis	X	X	X	X	X	X		X			X	X	Ann.	1, 2, 4
Ulothrix speciosa (Carm. *ex* Harv. *in* Hook.) Kütz.		X	X	X	X								Ann.	1, 2, 4
Ulva lactuca L.	X	X	X	X	X	X	X	X	X	X	X	X	Ann. or PPer.	1–4
Ulvaria obscura (Kütz.) Gayral	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1–4
Ulvaria oxysperma (Kütz.) Bliding	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1–4
Urospora penicilliformis (Roth) Aresch.	X	X	X	X	X	X	X	X		X	X	X	Ann.	1, 2, 4
Urospora wormskioldii (Mert. *in* Hornem.) Rosenv.	X	X	X	X	X		X	X*				X	Ann.	1, 2, 4
Monthly total Chlorophyta taxa	24	32	36	34	33	36	42	40	30	37	34	27		

Table II: Seasonal occurrence, longevity and local distribution of Phaeophyceae

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Agarum cribrosum (Mert.) Bory	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Alaria esculenta (L.) Grev.		X	X	X	X	X	X	X	X	X	X		Per.	1, 2
Ascocyclus distromaticus Tayl.	X			X	X		X	X	X				Ann.	1, 2
Ascophyllum nodosum (L.) Le Jol.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1-4
Ascophyllum nodosum (L.) Le Jol. ecad *scorpioides* (Reinke) Hauck	X	X	X	X	X	X	X	X	X	X	X	X	Per.	3, 4
Asperococcus fistulosus (Huds.) Hook.				X		X	X	X	X				Ann.	1, 2
Chorda filum (L.) Stackh.					X	X	X	X	X		X		Ann.	1-4
Chorda tomentosa Lyngb.				X	X	X		X					Ann.	1, 2, 4
Chordaria flagelliformis (O. F. Müll.) C. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1-4
Cladostephus spongiosus (Huds.) C. Ag. forma *verticillatus* (Lightf.) Post. et Rupr.		X											Per. (?)	1
Delamara attenuata (Kjellm.) Rosenv.				X	X	X					X		Ann.	1, 4
Desmarestia aculeata (L.) Lamour.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Desmarestia viridis (O. F. Müll.) Lamour.	X	X	X	X	X	X	X	X	X				Ann.	1, 2, 4
Desmotrichum undulatum (J. Ag.) Reinke				X	X	X*		X					Ann.	1, 2*, 4
Dictyosiphon foeniculaceus (Huds.) Grev.			X	X	X	X	X	X	X	X			Ann.	1-4
Ectocarpus fasciculatus Harv.				X	X	X	X	X	X	X			Ann.	1, 2, 4
Ectocarpus siliculosus (Dillw.) Lyngb.	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1-4

Table II: (Cont.)

Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Longevity	Local Distribution
	Month													
Elachista fucicola (Vell.) Aresch.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Eudesme virescens (Carm. *ex* Harv. *in* Hook.) J. Ag.							X						Ann.	2
Fucus distichus L. subsp. *anceps* (Harv. *et* Ward *ex* Carr.) Powell	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1
Fucus distichus L. subsp. *distichus* L. emend. Powell	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Fucus distichus L. subsp. *edentatus* (Pyl.) Powell	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Fucus distichus L. subsp. *evanescens* (C. Ag.) Powell	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Fucus spiralis L.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Fucus vesiculosus L.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Giffordia granulosa (Sm.) Hamel		X			X	X	X	X	X	X	X	X	Ann.	1–4
Giffordia sandriana (Zanar.) Hamel								X	X				Ann.	2, 4
Giffordia secunda (Kütz.) Batt.								X					Ann.	2
Hecatonema terminalis (Kütz.) Kylin													Ann.	2?
Isthmoplea sphaerophora (Carm. *ex* Harv. *in* Hook.) Kjellm.				X	X	X	X*	X					Ann.	1, 2*, 4
Laminaria digitata (Huds.) Lamour.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4

Table II: (Cont.)

	Month													Local
Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Longevity	Distribution
Laminaria longicruris Pyl.		X	X	X	X	X	X	X	X	X	X		Per.	1, 2, 4
Lamanaria saccharina (L.) Lamour.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1 4
Laminariocolax tementosoides (Farl.) Kylin			X	X				X		X		X	Ann. (?)	1, 2
Leathesia difformis (L.) Aresch.				X	X	X	X	X	X	X	X		Ann.	1, 2
Mikrosyphar porphyrae Kuck.					X		X	X					Ann.	1 (+ Cape Neddick, ME)
Myrionema corunnae Sauv.		X	X	X	X	X	X	X	X	X	X		Ann.	1, 2, 4
Myrionema magnusii (Sauv.) Lois.													Ann.	2?
Myrionema strangulans Grev.						X	X	X					Ann.	1, 2, 4
Petalonia fascia (O. F. Müll.) Kuntze	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1–4
Petalonia zosterifolia (Reinke) Kuntze			X	X	X			X			X	X	Ann.	1, 2, 4
Petroderma maculiforme (Wolny) Kuck.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	2, 4
Pilayella littoralis (L.) Kjellm.	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1 4
Protectocarpus speciosus (Børgesen) kuck.		X	X	X	X	X	X		X	X	X		Ann. (?)	1, 2
Pseudolithoderma extensum (Crouan frat.) S. Lund	X	X	X	X	X	X	X	X	X	X	X		Per.	1, 2, 4
Punctaria latifolia Grev.						X	X	X	X	X			Ann.	4
Punctaria plantaginea (Roth) Grev.						X	X	X					Ann.	1, 2
"*Ralfsia bornetii* Kuck."		X	X	X	X	X		X	X		X		Per. (?)	1 4

Table II: (Cont.)

	Month													Local
Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Longevity	Distribution
"*Ralfsia clavata* (Harv. *in* Hook.) Crouan frat."			X	X		X	X	X	X	X	X	X	Per. (?)	1-4
Ralfsia fungiformis (Gunn.) Setch. *et* Gardn.		X			X	X	X	X		X			Per.	2, 4
Ralfsia verrucosa (Aresch.) J. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1-4
Saccorhiza dermatodea (Pyl.) J. Ag.					X	X	X	X					Ann.	1, 2
Scytosiphon lomentaria (Lyngb.) Link var. *complanatus* Rosenv.		X	X										Ann.	4
Scytosiphon lomentaria (Lyngb.) Link var. *lomentaria*	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1-4
Sorapion kjellmanii (Wille) Rosenv.								X					Per.	2 (+ York River, ME)
Sorocarpus micromorus (Bory) Silva						X							Ann.	4
Sphacelaria arctica Harv.				X			X	X	X		X		Per. (?)	2
Sphacelaria cirrosa (Roth) C. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Sphacelaria fusca (Huds.) S. F. Gray							X						Per. (?)	1
Sphacelaria plumigera Holmes							X	X					Per.	2
Sphacelaria plumosa Lyngb.							X	X	X				Per. (?)	2
Sphacelaria radicans (Dillw.) C. Ag.	X	X	X		X	X	X	X	X	X	X		Per.	2, 3
Sphaerotrichia divaricata (C. Ag.) Kylin											X*		Ann.	2*
Spongonema tomentosum (Huds.) Kütz.)		X	X	X	X		X	X	X	X	X		Per. (?)	1, 2, 4

Table II: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Stictyosiphon griffithsianus (Le Jol.) Holm. *et* Batt.					X	X							Ann.	4
Ulonema rhizophorum Fosl.		X	X	X	X	X	X	X			X		Ann.	1, 2, 4
Montly total Phaeophyta taxa	25	34	36	43	46	48	50	55	42	36	38	27		

Table III: Seasonal occurrence, longevity and local distribution of Rhodophyceae

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Ahnfeltia plicata (Huds.) Fries	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Antithamnion cruciatum (C. Ag.) Näg.		X	X	X	X	X	X	X	X	X	X	X	Ann.	2, 4
Antithamnionella floccosa (O. F. Müll.) Whittick	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1, 2, 4
Audouinella alariae (Jónss.) Woelk.						X	X	X			X		Ann.	1, 2
Audouinella membranacea (Magn.) Papenf.	X	X	X	X	X	X	X	X	X	X	X	X	Per. (?)	1, 2, 4
Audouinella polyides (Rosenv.) Garbary									X				Ann.	2
Audouinella purpurea (Lightf.) Woelk.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Audouinella secundata (Lyngb.) Dixon	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1–4
Audouinella violaceae (Kütz.) Hamel			X		X	X	X	X	X	X	X	X	Ann.	4
Bangia atropurpurea (Roth) C. Ag.	X	X	X	X	X	X		X			X	X	Ann.	1, 2, 4
Bonnemaisonia hamifera Hariot			X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Callithamnion byssoides Arnott *ex* Harv. *in* Hook.									X	X			Ann.	4
Callithamnion hookeri (Dillw.) S. F. Gray							X	X	X				Ann.	1, 2, 4
Callithamnion tetragonum (With.) S. F. Gray	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Callocolax neglectus Schm. *ex* Batt.		X	X	X	X	X	X	X	X	X	X		Per. (?)	1, 2, 4
Callophyllis cristata (C. Ag.) Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Ceramium deslongchampii Chauv. *in* Duby var. *hooperi* (Harv.) Tayl.		X		X	X	X	X	X	X	X	X		Per. (?)	1, 2, 4

Table III: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Ceramium elegans (Ducluz.) C. Ag.								X					Ann.	4
Ceramium rubrum (Huds.) C. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Ceramium strictum Harv.		X			X	X	X	X	X	X	X	X	Ann.	2 4
Ceratocolax hartzii Rosenv.	X	X	X	X	X		X	X	X	X	X	X	Per.	1, 2
Chondria baileyana (Mont.) Harv.						X	X	X	X	X	X		Ann.	2, 4
Chondrus crispus Stackh.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Choreocolax polysiphoniae Reinsch	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Clathromorphum circumscriptum (Strömf.) Fosl.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Corallina officinalis L.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
"*Cruoriopsis ensis* Jao"							X				X		Per. (?)	2, 4
Cystoclonium purpureum (Huds.) Batt.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Dasya baillouviana (Gmel.) Mont.	X**	X**				X	X	X	X	X	X	X	Ann.	4
Dermatolithon pustulatum (Lamour.) Fosl.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Devaleraea ramentaceum (L.) Guiry	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2
Dumontia contorta (Gmel.) Rupr.	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1–4
Erythropeltis discigera (Berth.) Schm. var. *discigera*		X						X					Ann.	1, 2
Erythrotrichia carnea (Dillw.) J. Ag.		X		X		X	X	X	X	X	X		Ann.	1 4

Table III: (Cont.)

	Month													Local
Taxa	J	F	M	A	M	J	J	A	S	O	N	D	Longevity	Distribution
Fosliella lejolisii (Rosan.) Howe	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Gigartina stellata (Stackh.) Batt.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Gloiosiphonia capillaris Carm. *in* Berk.					X	X	X	X					Ann.	1, 2, 4
Goniotrichum alsidii (Zanard.) Howe				X				X	X	X	X		Ann.	1, 4
Gracilaria tikvahiae McLachlan	X	X	X	X	X	X	X	X	X	X	X	X	Per.	4
Gymnogongrus crenulatus (Turn.) J. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Halosacciocolax kjellmanii S. Lund					X								Per. (?)	1
Harveyella mirabilis (Reinsch.) Schm. *et* Reinke *in* Reinke						X			X	X	X		Per.	1, 2
Hildenbrandia rubra (Sommerf.) Menegh.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Leptophytum foecundum (Kjellm.) Adey	X	X		X	X	X	X	X	X	X	X	X	Per.	1, 2
Leptophytum laeve (Strömf.) Adey	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Lithophyllum corallinae (Crouan frat.) Heydr.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Lithothamnion glaciale Kjellm.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Lomentaria baileyana (Harv.) Farl.						X	X	X	X	X	X	X	Ann.	4
Lomentaria clavellosa (Turn.) Gaillon	X	X		X	X	X	X	X	X	X	X	X	Per. (?)	4 (+ Boone I., Maine
Lomentaria orcadensis (Harv.) Coll. *ex* Tayl.				X			X	X	X	X	X		Per	1, 2, 4
Membranoptera alata (Huds.) Stackh.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4

Table III: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Nemalion helminthoides (Vell. *in* With.) Batt.						X	X	X					Ann.	1, 2
Palmaria palmata (L.) O. Kuntze	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Pantoneura baeri (Post. *et* Rupr.) Kylin					X	X							Per.	1
"*Petrocelis cruenta* J. Ag."	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Peyssonnelia rosenvingii Schm. *in* Rosenv.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Phycodrys rubens (L.) Batt.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Phyllophora pseudoceranoides (Gmel.) New. *et* A. Tayl.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Phyllophora traillii Holm. *ex* Batt.						X	X	X		X	X		Per.	1, 2
Phyllophora truncata (Pallas) A. Zin.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Phymatolithon laevigatum (Fosl.) Fosl.		X		X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Phymatolithon lenormandii (Aresch. in J. Ag.) Adey	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Phymatolithon rugulosum Adey					X	X	X	X			X	X	Per.	1, 2
Plumaria elegans (Bonnem.) Schm.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–3
Polyides rotundus (Huds.) Grev.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Polysiphonia denudata (Dillw.) Kütz.		X		X		X	X	X	X	X	X	X	Ann.	3, 4
Polysiphonia elongata (Huds.) Spreng.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	2–4

Table III: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Polysiphonia flexicaulis (Harv.) Coll.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Polysiphonia harveyi Bailey	X	X				X	X	X	X	X	X	X	Ann.	1, 2, 4
Polysiphonia lanosa (L.) Tandy	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Polysiphonia nigra (Huds.) Batt.	X	X	X	X	X	X	X	X	X	X	X	X	Per. (?)	1–4
Polysiphonia nigrescens (Huds.) Grev.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Polysiphonia novae-angliae Tayl.	X							X				X	Per. (?)	1, 2
Polysiphonia subtilissima Mont.			X	X	X	X	X	X	X	X	X	X	Per.	3, 4
Polysiphonia urceolata (Lightf. *ex* Dillw.) Grev.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Porphyra leucosticta Thur. *in* Le Jol.	X	X	X	X	X	X	X	X	X		X	X	Ann.	1, 2, 4
Porphyra linearis Grev.	X	X	X	X	X					X		X	Ann.	1, 2, 4
Porphyra miniata (C. Ag.) J. Ag.			X	X	X	X	X	X	X				Ann.	1, 2, 4
Porphyra umbilicalis (L.) J. Ag.	X	X	X	X	X	X	X	X	X	X	X	X	Ann.	1–4
"*Porphyrodiscus simulans* Batt."											X		Per. (?)	4
Porphyropsis coccinea (J. Ag. *ex* Arsesch.) Rosenv.		X						X			X*		Ann.	2
Pterothamnion plumula (Ellis) Näg.	X		X			X	X	X	X	X		X	AAnn.	1, 2, 4
Ptilota serrata Kütz.	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1–4
Rhodomela confervoides (Huds.) Silva		X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Rhodophyllis dichotoma (Lepesch.) Gobi	X	X	X	X	X	X	X	X	X	X			Per.	1, 2, 4

Table III: (Cont.)

Taxa	Month												Longevity	Local Distribution
	J	F	M	A	M	J	J	A	S	O	N	D		
Rhodophysema elegans (Crouan frat. *ex* J. Ag.) Dixon	X	X	X	X	X	X	X	X	X	X	X	X	Per.	1, 2, 4
Rhodophysema georgii Batt.		X	X	X	X		X	X	X				Per. (?)	4
Sacheria fucina (Bory) Sirodot	X	X		X	X	X	X	X	X	X	X	X	Per.	4
Scagelia corallina (Rupr.) Hansen *et* Scagel	X	X	X	X	X	X	X	X	X	X	X	X	AAnn.	1, 2, 4
Spermothamnion repens (Dillw.) Rosenv.			X					X		X			Ann.	1, 2
"*Trailliella intricata* Batt."			X	X		X	X	X		X	X		Per.	1, 4
Turnerella pennyi (Harv.) Schm.											X	X	Per.	2
Monthly total Rhodophyta taxa	56	65	60	66	67	75	77	83	74	73	76	66		
Monthly grand total seaweed taxa	105	131	132	143	146	159	169	178	146	146	148	120		

Table IV: Summary of collection sites

Geographical Area	No. and/or Names of Permanent Stations	Sites with at Least 2 yrs. of Seasonal Collections	Sites with at Least 2 yrs. of Monthly Collections	Pertinent References
1. Isles of Shoals				Mathieson (1979)
				Mathieson & Penniman (1986a)
				Norall et al. (1981)
	Appledore Island	X		
	Cedar Island	X		
	Duck Island	X		
	Lunging Island	X		
	Malaga Island	X		
	Smuttynose Island	X		
	Star Island	X		
	White Island	X		
2. Nearshore open coast	13 sites		X	Hehre & Mathieson
	Jaffrey Point, New Castle		X	Mathieson, Hehre, & Reynolds (1981)
	43°03′22″N, 70°42′49″W			Mathieson & Penniman (1986a,b)
				Mathieson, Reynolds & Hehre (1981)
	Bound Rock, Seabrook		X	Daly & Mathieson (1977)
	42°53′30″N, 70°48′45″W			Mathieson & Fralick (1972)
				Mathieson & Penniman (1986a,b)
3. Hampton-Seabrook Estuary System	49 total sites	X		Mathieson and Fralick (1972)
	Blackwater River—11 sites	X		
	Brown River—13 sites	X		

Table IV (Continued)

Geographical Area	No. and/or Names of Permanent Stations	Sites with at Least 2 yrs. of Seasonal Collections	Sites with at Least 2 yrs. of Monthly Collections	Pertinent References
	Hampton River—18 sites	X		
	Hampton Harbor—7 sites	X		
4. Great Bay Estuary System				Mathieson, Reynolds, & Hehre (1981)
	182 total sites	X		
	Great Bay—16 sites	X		
	Crommet Creek, Durham 43°05′52″N, 70°53′53″W		X	Daly & Mathieson (1981) Mathieson & Penniman (1986b)
	Nannies Island, Newington 43°04′08″N, 70°51′47″W		X	Mathieson & Penniman (1986b)
	Thomas Point, Newington 43°04′53″N, 70°51′56″W		X	Mathieson & Penniman (1986b)
	Weeks Point, Greenland 43°03′32″N, 70°51′42″W		X	Mathieson, Reynolds & Hehre (1981)
	Little Bay—21 sites	X		
	Adams Point, Durham 43°05′43″N, 70°52′07″W		X	Mathieson, Reynolds & Hehre (1981)
	Cedar Point, Durham 43°07′45″N, 70°51′08″W		X	Chock and Mathieson (1976, 1983) Mathieson & Penniman (1986b) Mathieson, Reynolds & Hehre (1981)
	Dover Point, Dover 43°07′07″N, 70°49′42″W		X	Mathieson et al. (1983) Mathieson & Penniman (1986a,b)

Table IV (Continued)

Geographical Area	No. and/or Names of Permanent Stations	Sites with at Least 2 yrs. of Seasonal Collections	Sites with at Least 2 yrs. of Monthly Collections	Pertinent References
	Durham Point, Durham 43°07′14″N, 70°52′10″W		X	Mathieson, Reynolds & Hehre (1981) Reynolds & Mathieson (1975) Mathieson & Penniman (1986b)
	Bellamy River—10 sites	X		
	Cocheco River—17 sites	X		
	Lamprey River 9 sites	X		
	Oyster River—14 sites	X		
	Headwater at route 108, Durham 43°07′52″N, 70°55′06″W		X	Mathieson & Penniman (1986b)
	Piscataqua River—59 sites	X		
	Atlantic Heights, Portsmouth 43°05′36″N, 70°46′08″W			Mathieson et al. (1977)
	Normandeau Schiller site #16, just east of the Schiller Power generating station, Portsmouth 43°05′41″N, 70°46′51″W		8 years of continuous seasonal collections	Normandeau Assoc. (1971-80)

Table IV (Continued)

Geographical Area	No. and/or Names of Permanent Stations	Sites with at Least 2 yrs. of Seasonal Collections	Sites with at Least 2 yrs. of Monthly Collections	Pertinent References
	Ibid., #17, at end of Long Reach Farm, Eliot, Maine 43°06′02″N, 70°46′52″W		8 years of continuous seasonal collections	Normandeau Assoc. (1971–80)
	Ibid., #20, near Schiller Power Plant, Newington 43°06′15″N, 70°47′47″W		8 years of continuous seasonal collections	Normandeau Assoc. (1971–80)
	Ibid., #40, near Simplex, Pier, Newington 43°06′15″N, 70°47′47″W		8 years of continuous seasonal collections	Mathieson & Penniman (1986b) Normandeau Assoc. (1971–80)
	Ibid. #44, area just west of Simplex Pier and Union Oil Terminal, Newington 43°06′28″N, 70°47′58″W		8 years of continuous seasonal collections	Normandeau Assoc. (1971–80)
	Salmon Falls River—16 sites	X		
	Squamscott River—16 sites			
	Chapman's Landing Route 108 bridge, Newfields 43°02′24″N, 70°55′43″W		X	Mathieson & Penniman (1986b) Mathieson, Reynolds & Hehre (1981)
	Winnicut River 4 sites	X		

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DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
JACKSON ESTUARINE LABORATORY
UNIVERSITY OF NEW HAMPSHIRE
DURHAM, NH 03824

FIGURES 16–229. SPECIES DISTRIBUTION MAPS FOR 214 TAXA FOUND WITHIN COASTAL-ESTUARINE WATERS OF NEW HAMSPHIRE AND SOUTHERN MAINE.

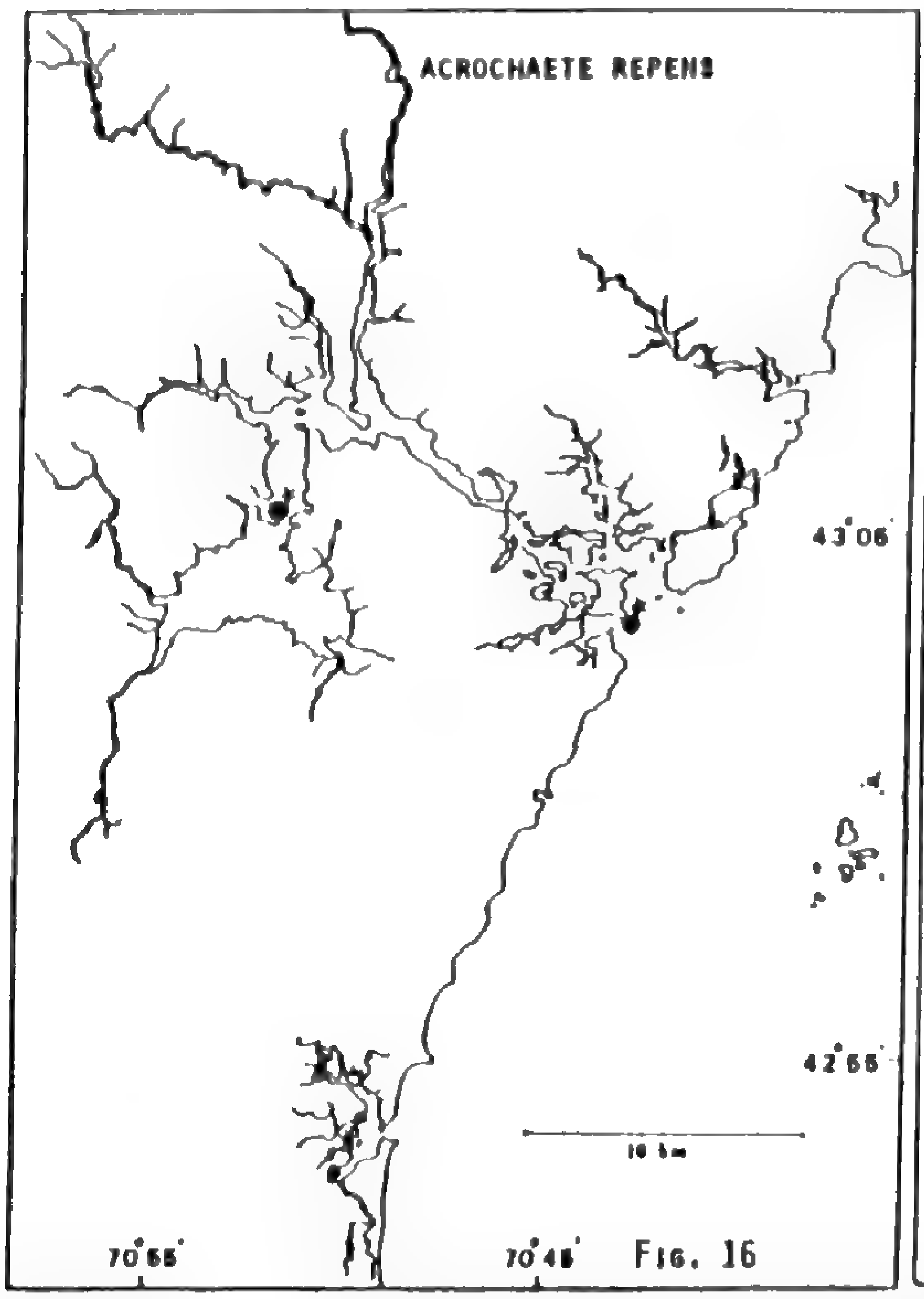


FIG. 16

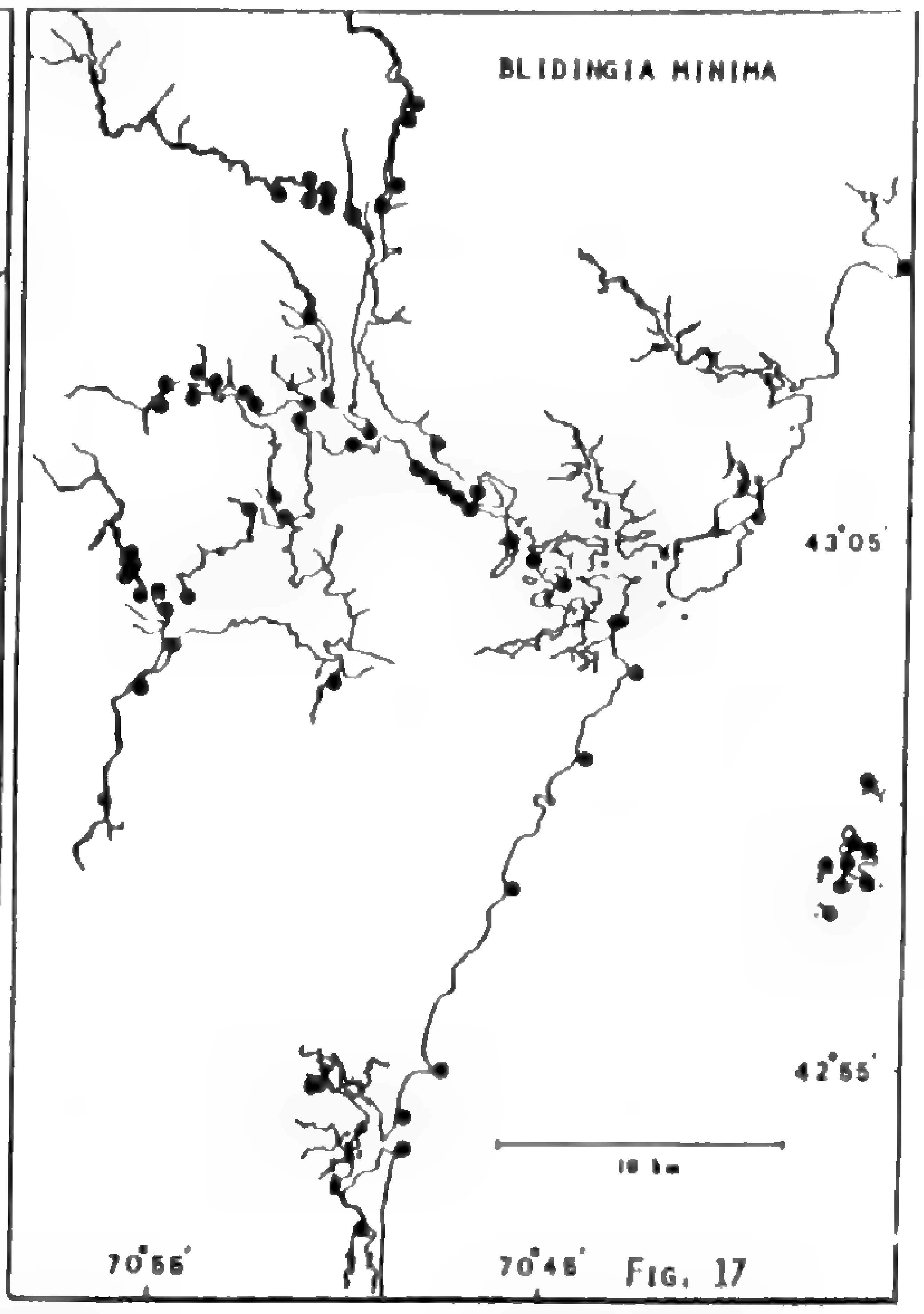


FIG. 17

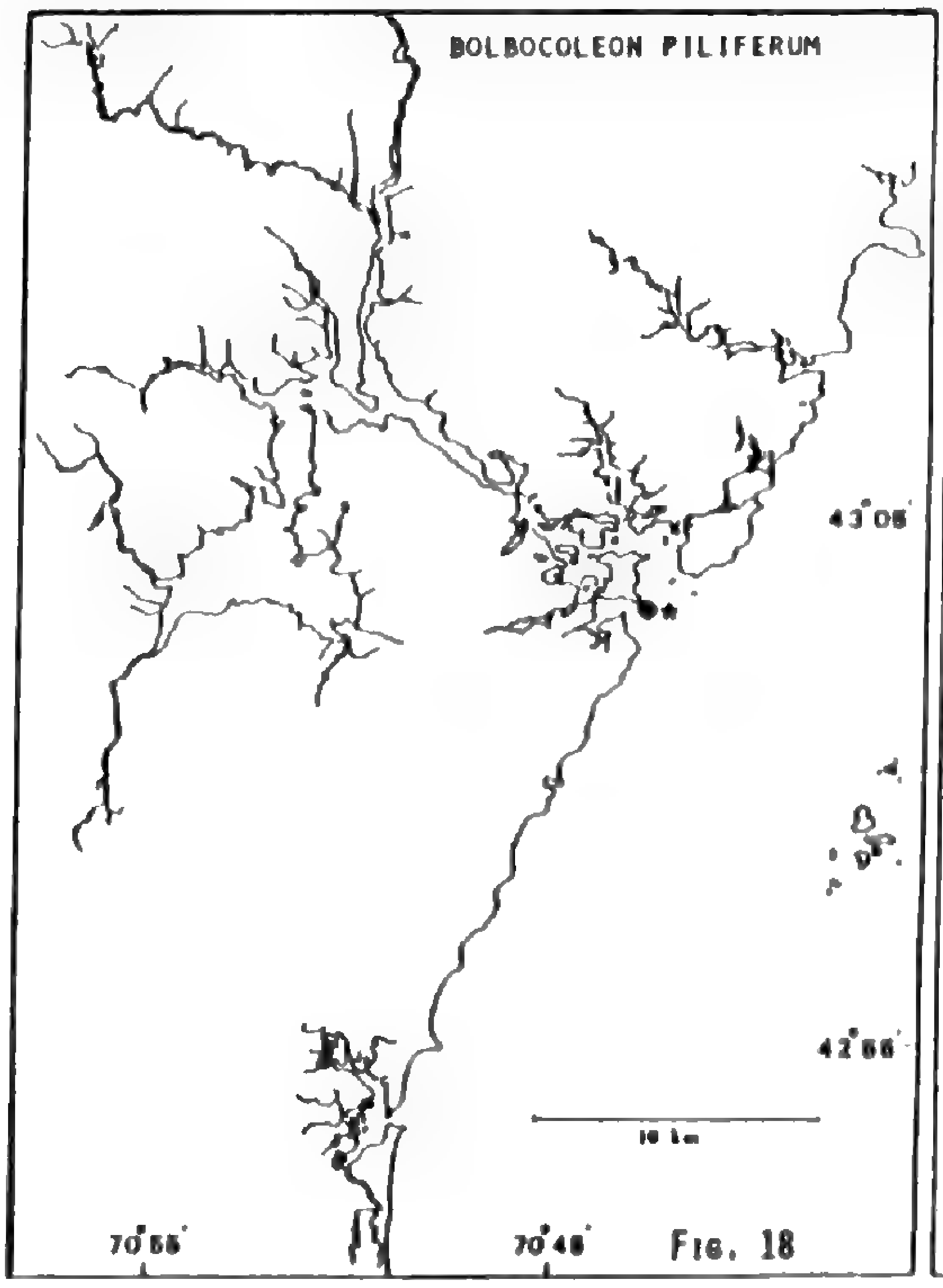


FIG. 18

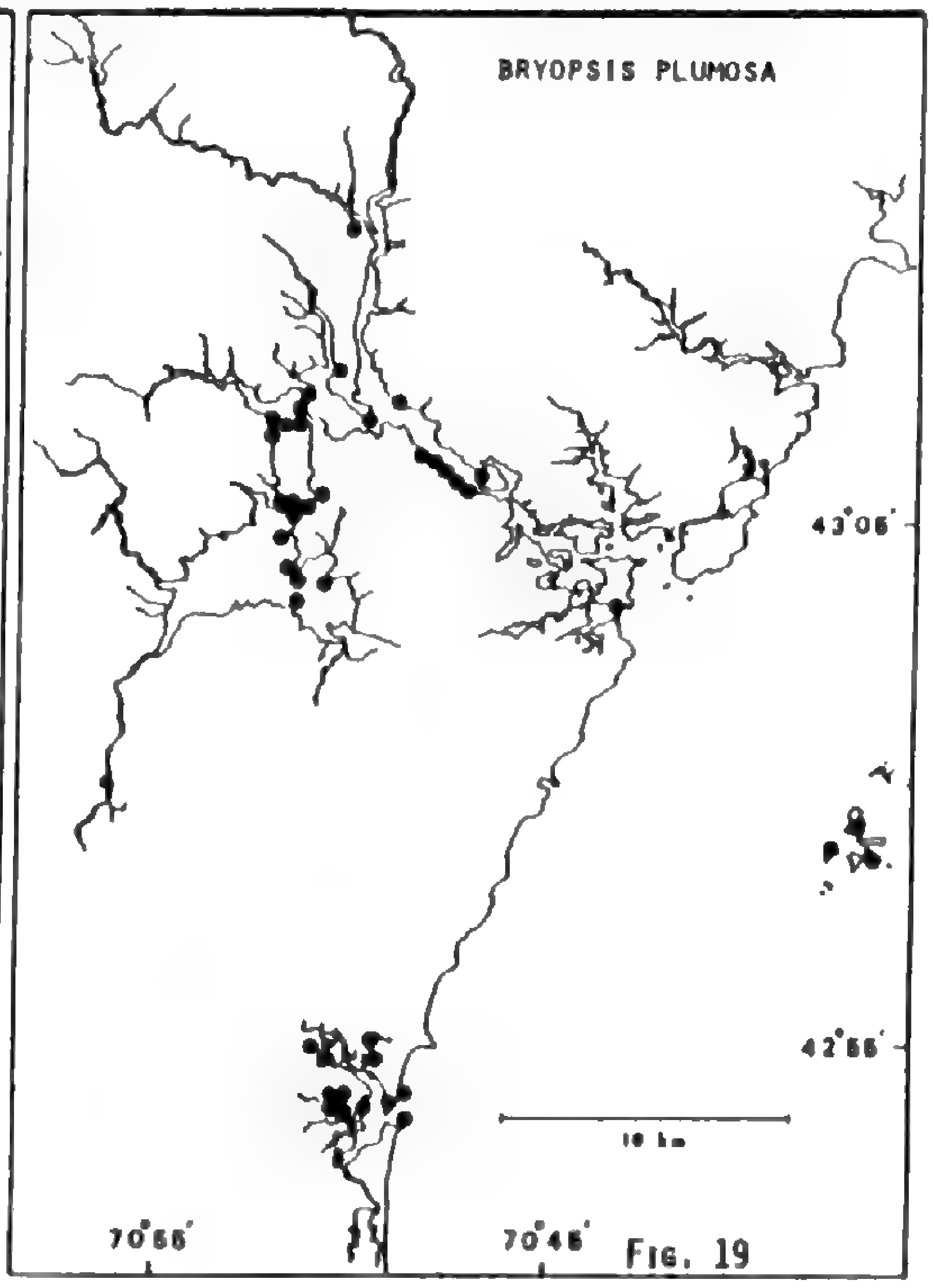


FIG. 19

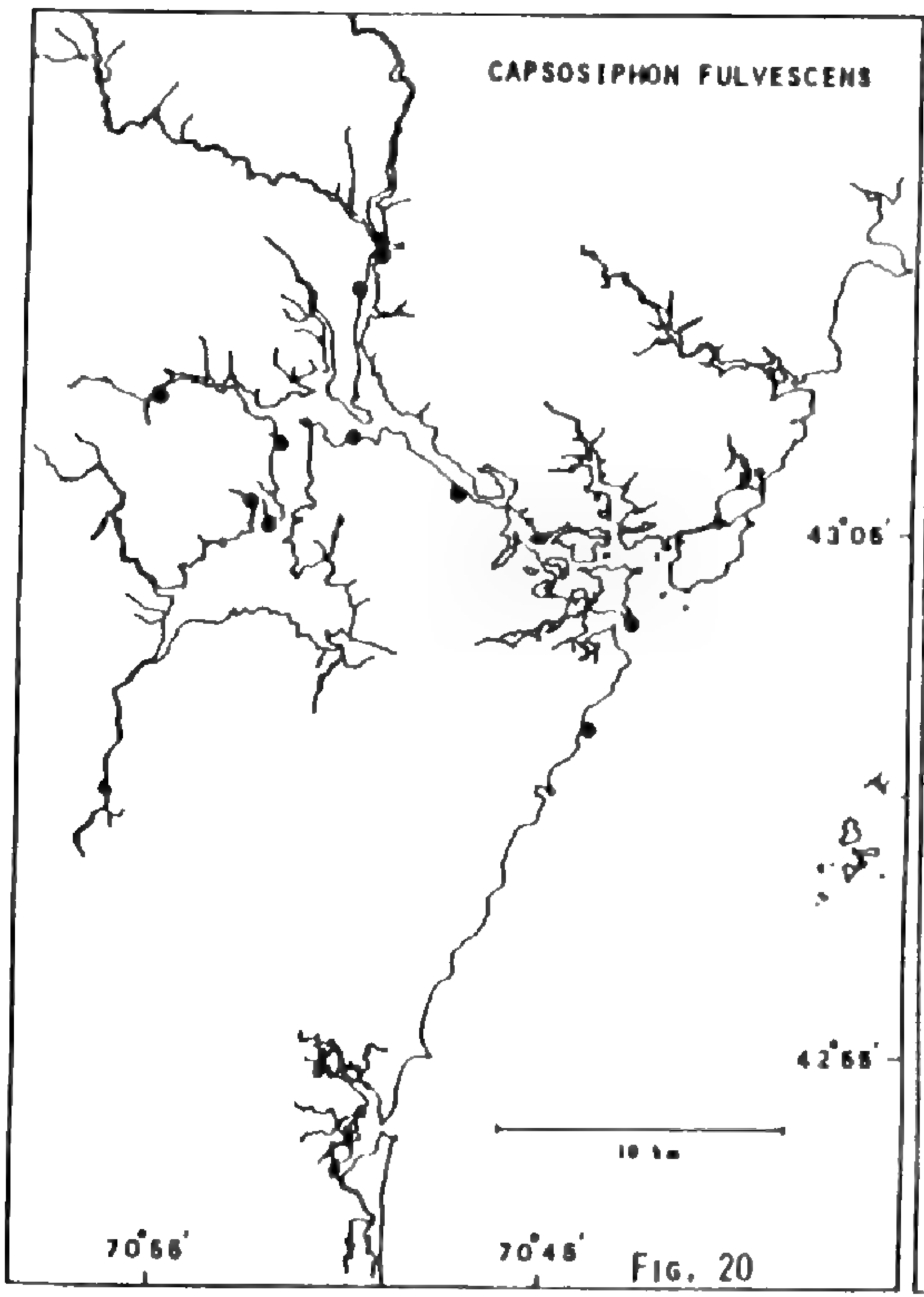


Fig. 20

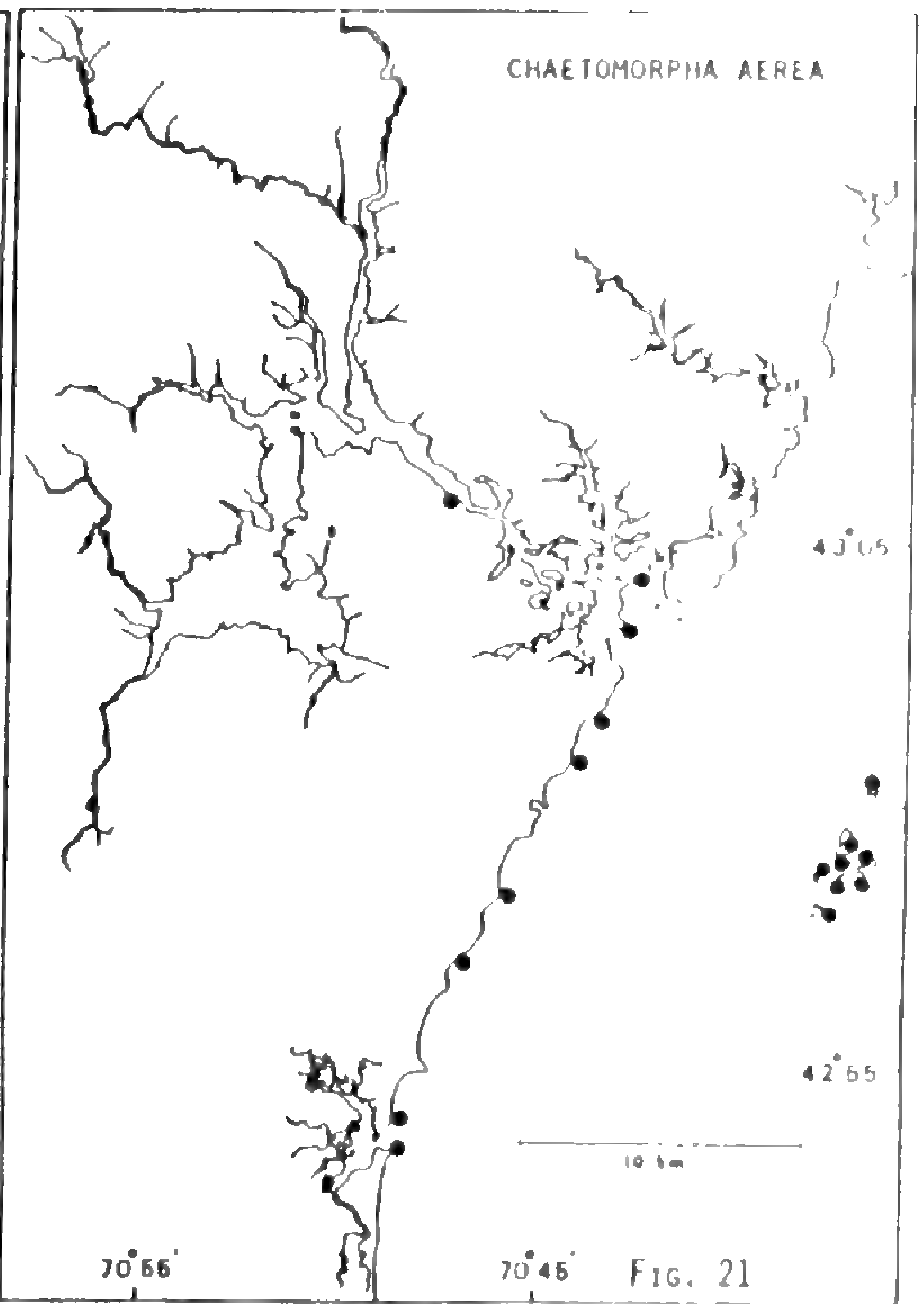


Fig. 21

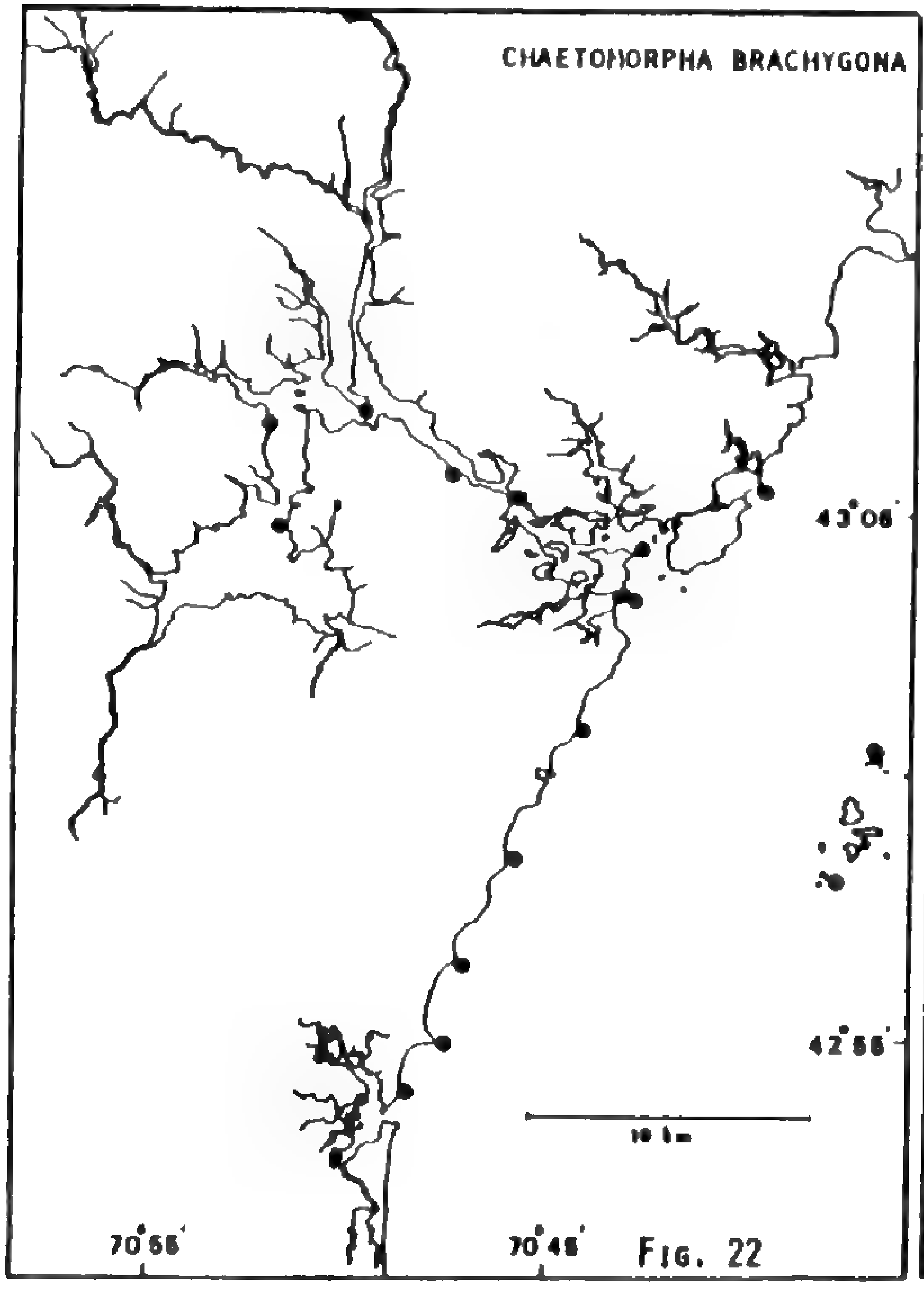


Fig. 22

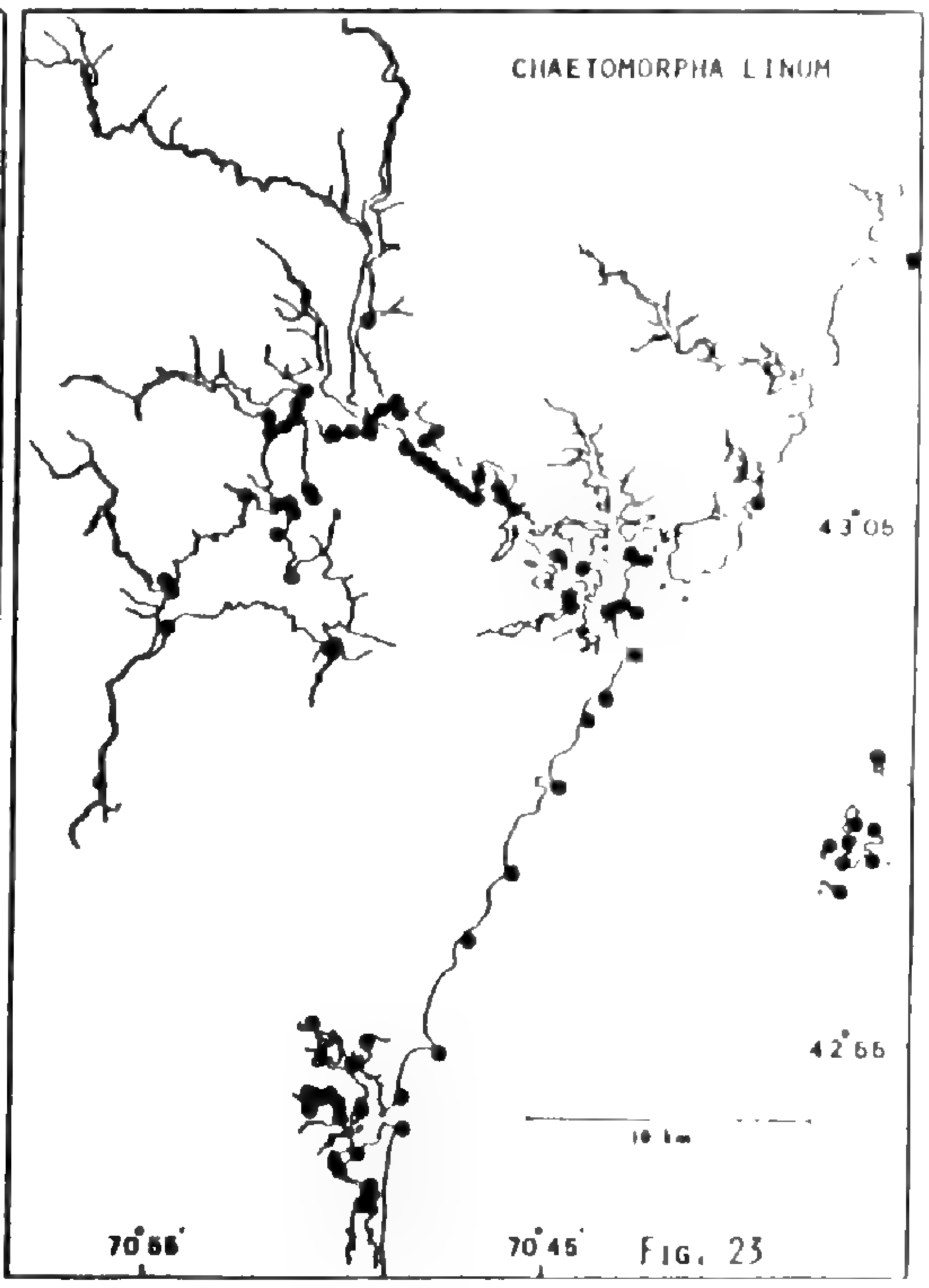


Fig. 23

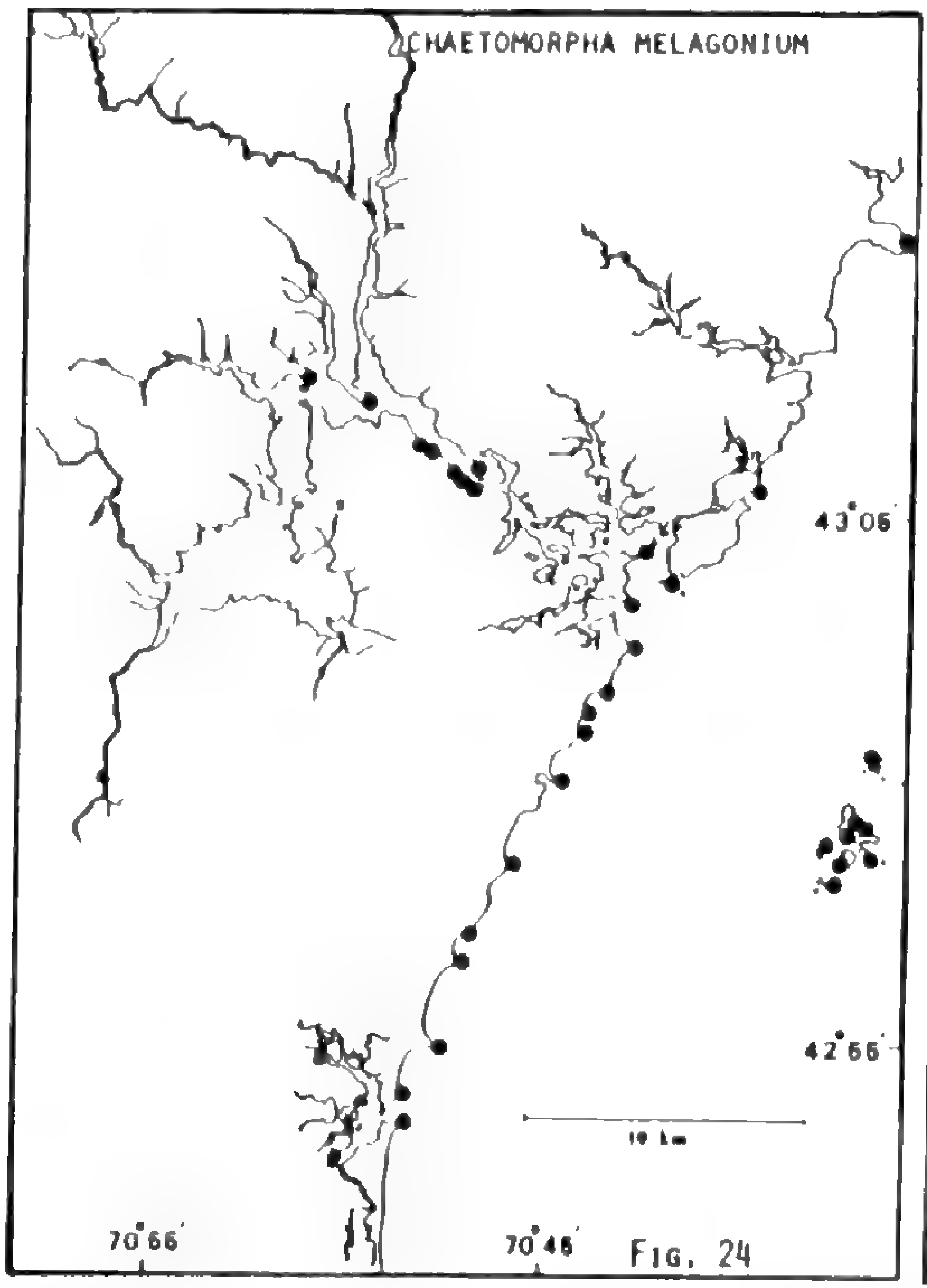


FIG. 24

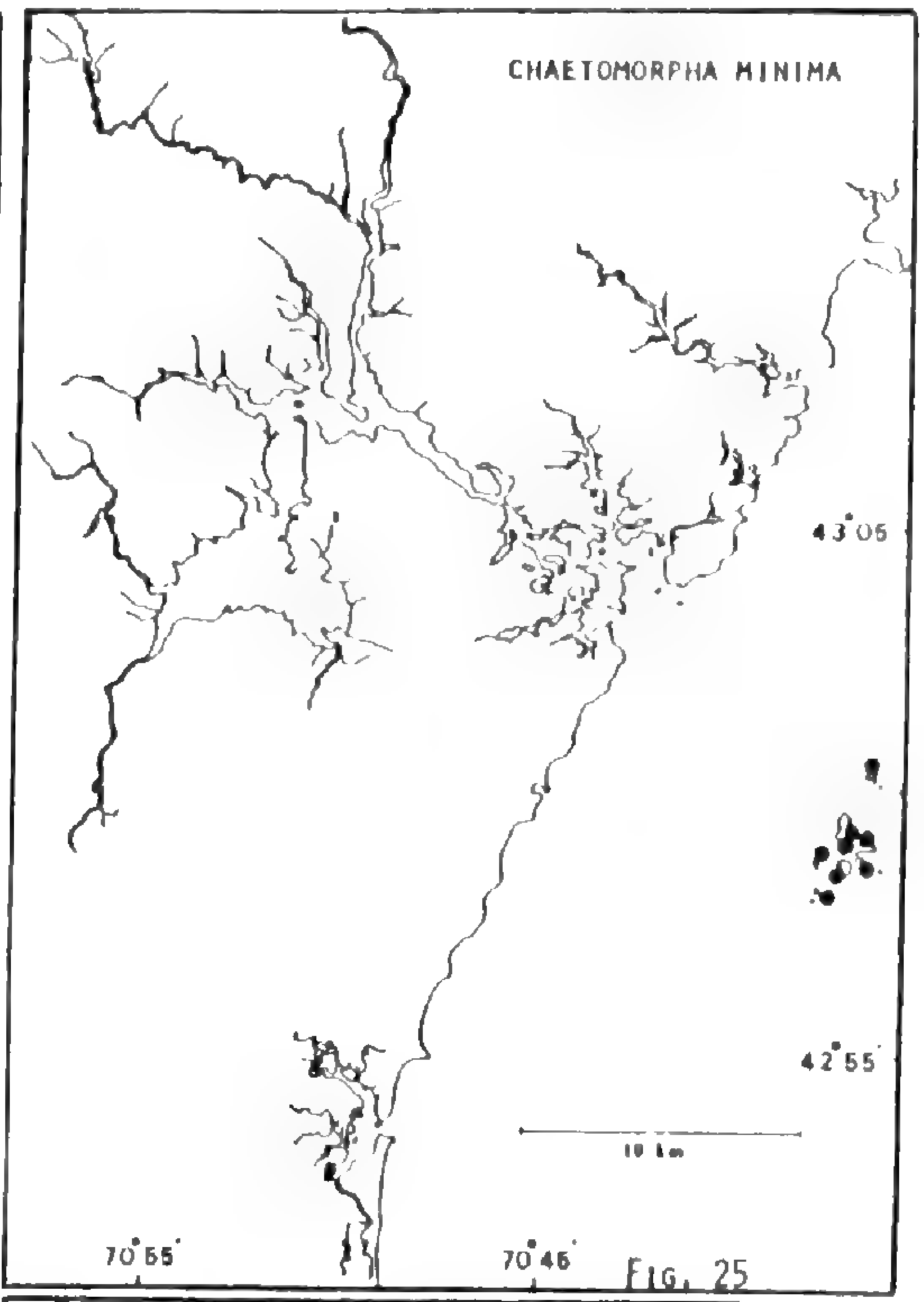


FIG. 25

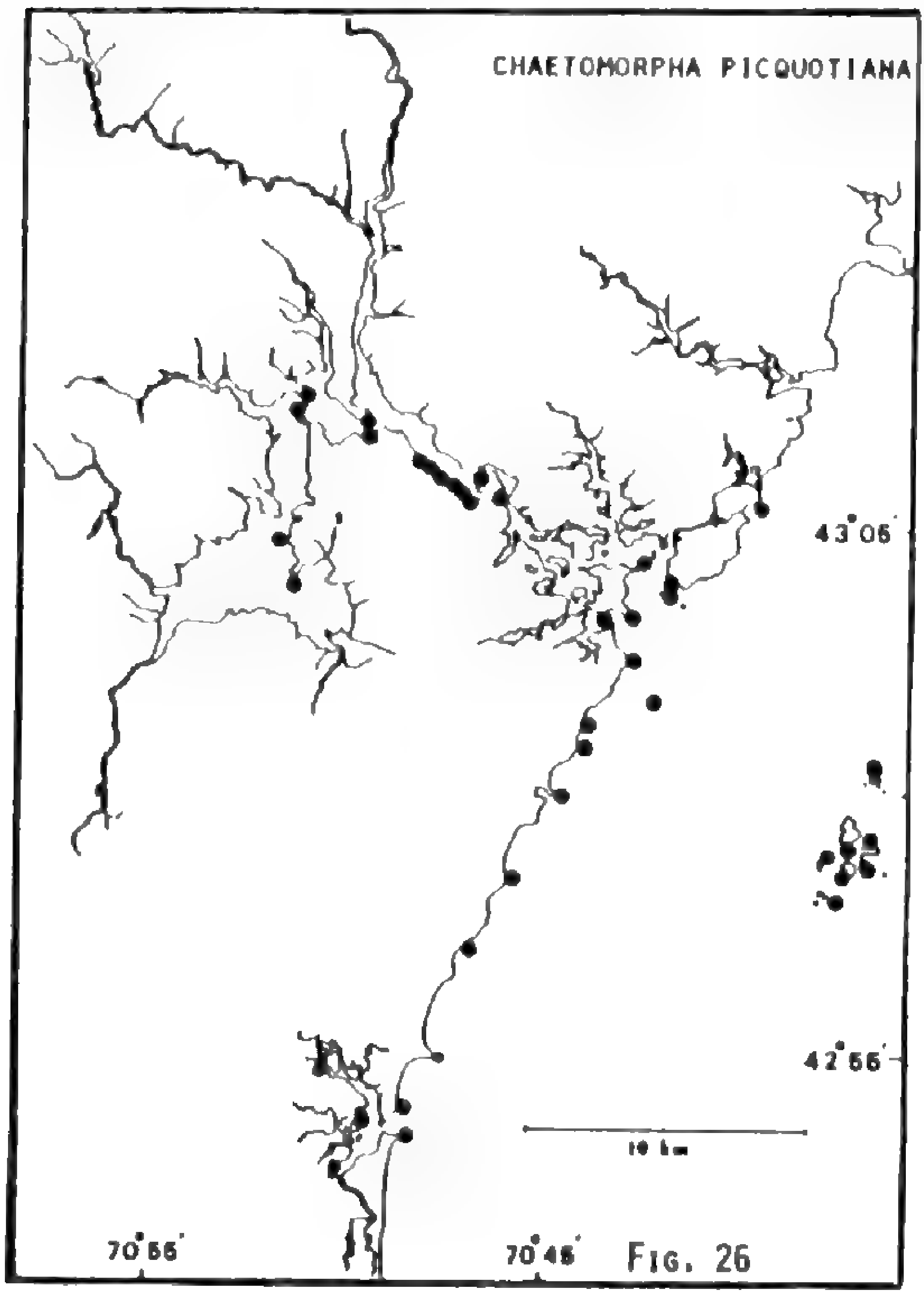


FIG. 26

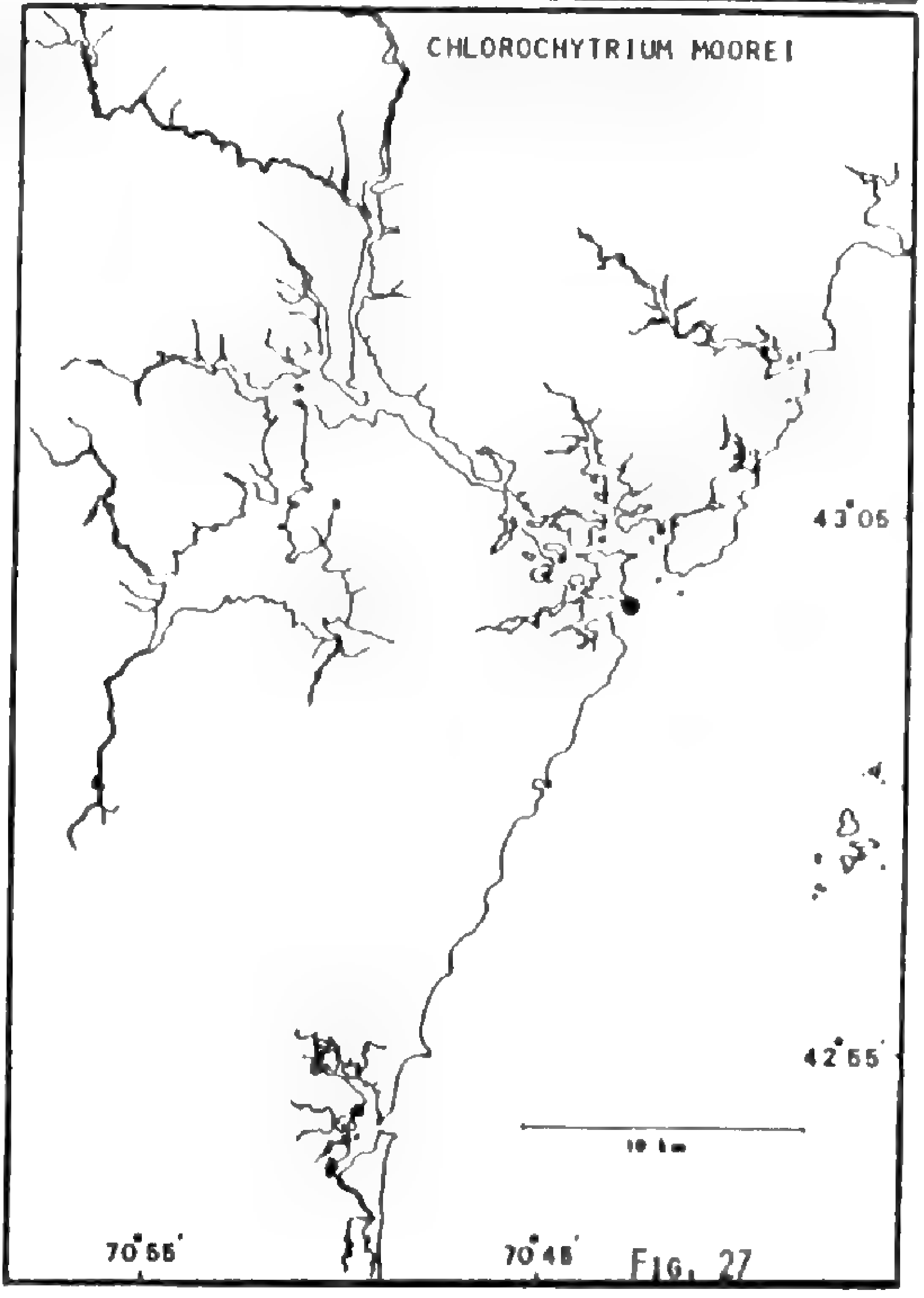


FIG. 27

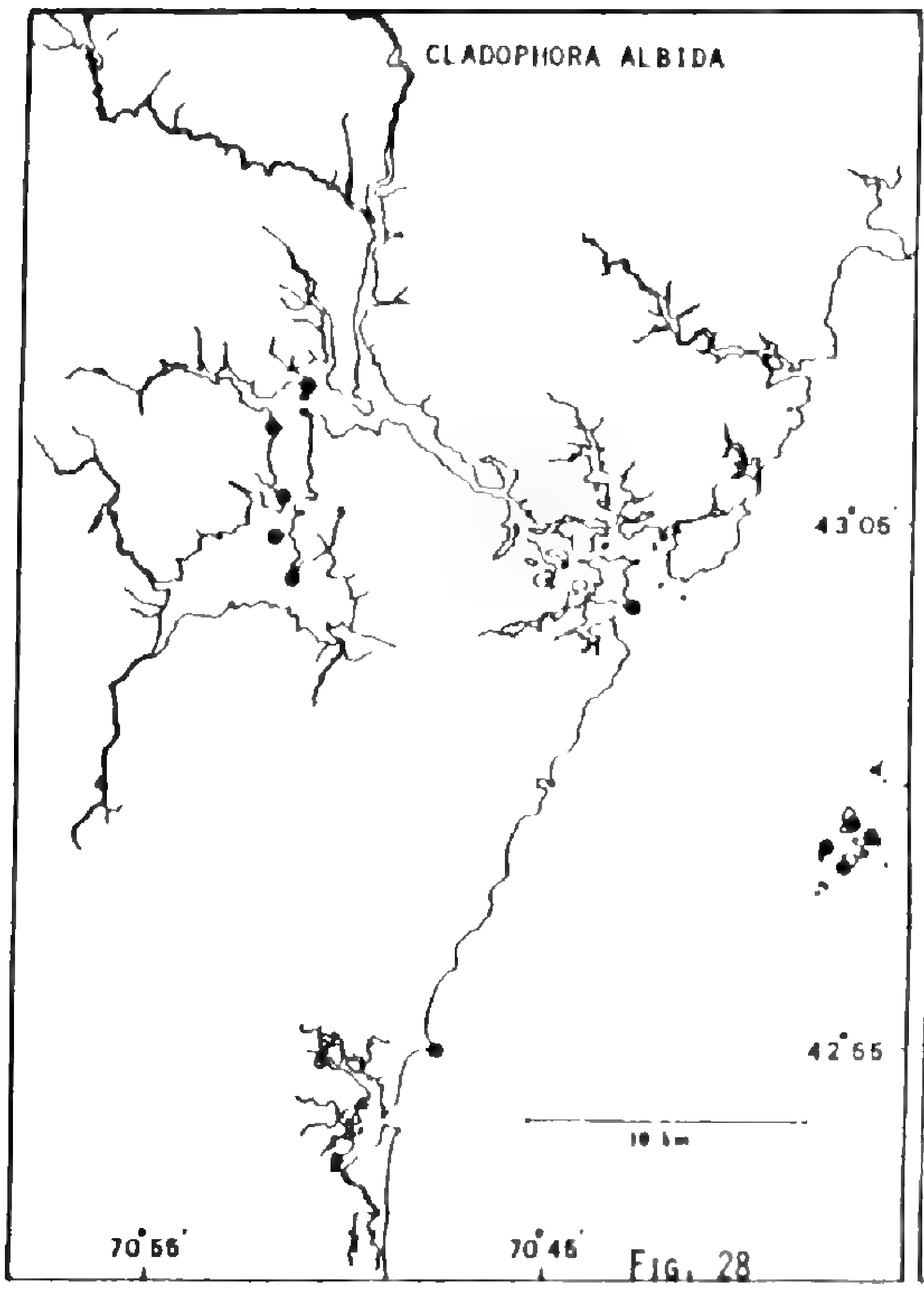


FIG. 28

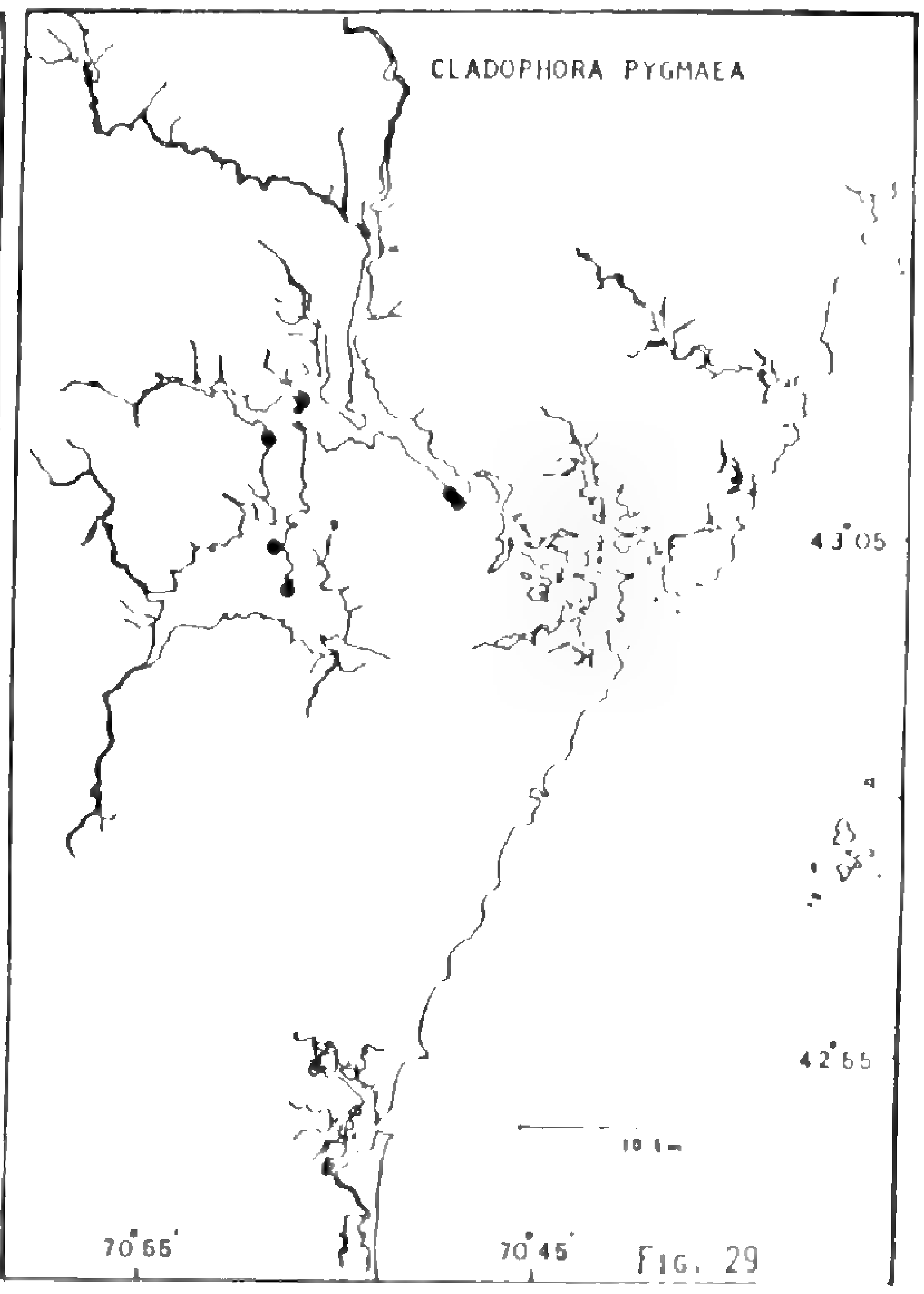


FIG. 29

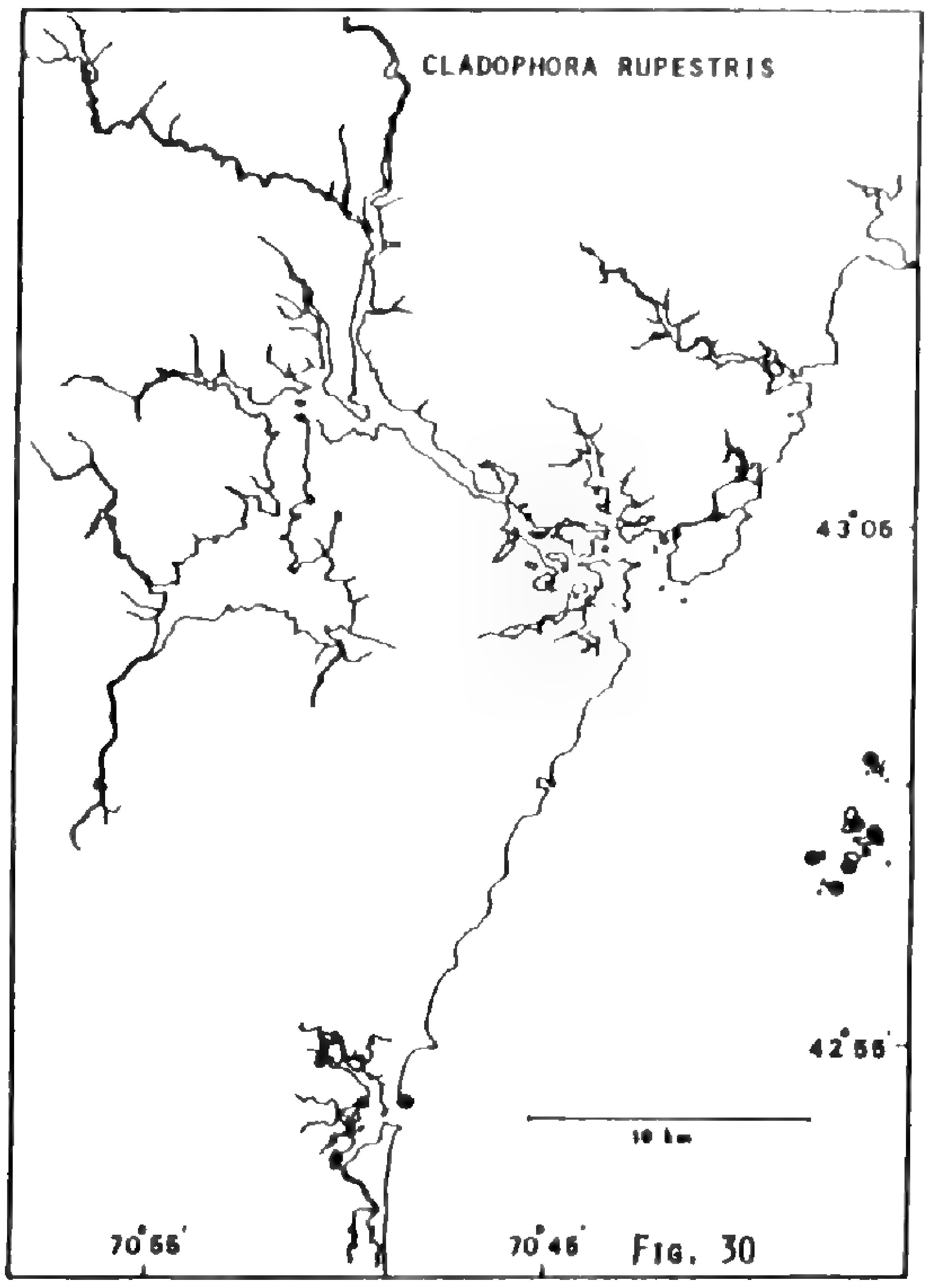


FIG. 30

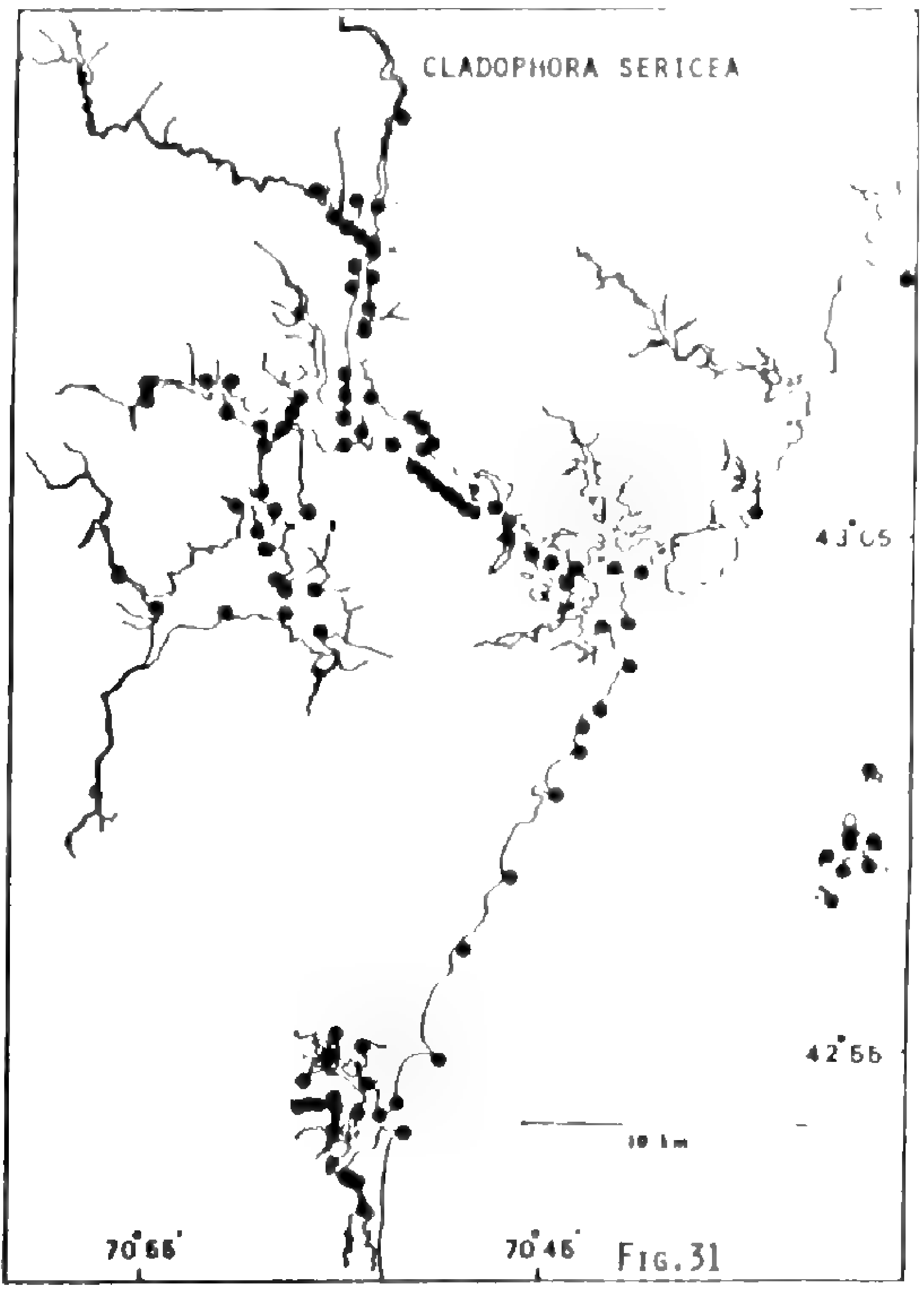


FIG. 31

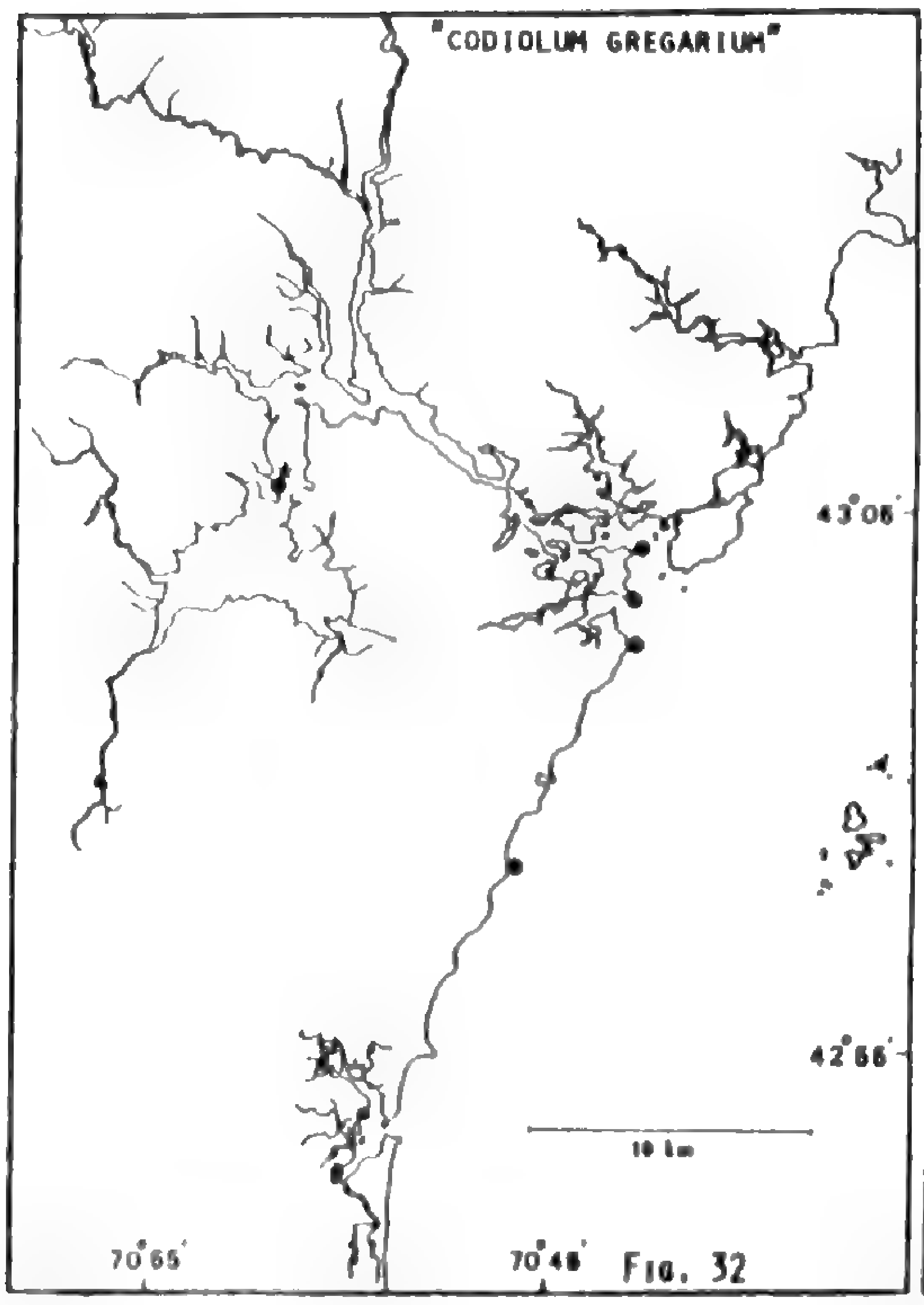


Fig. 32

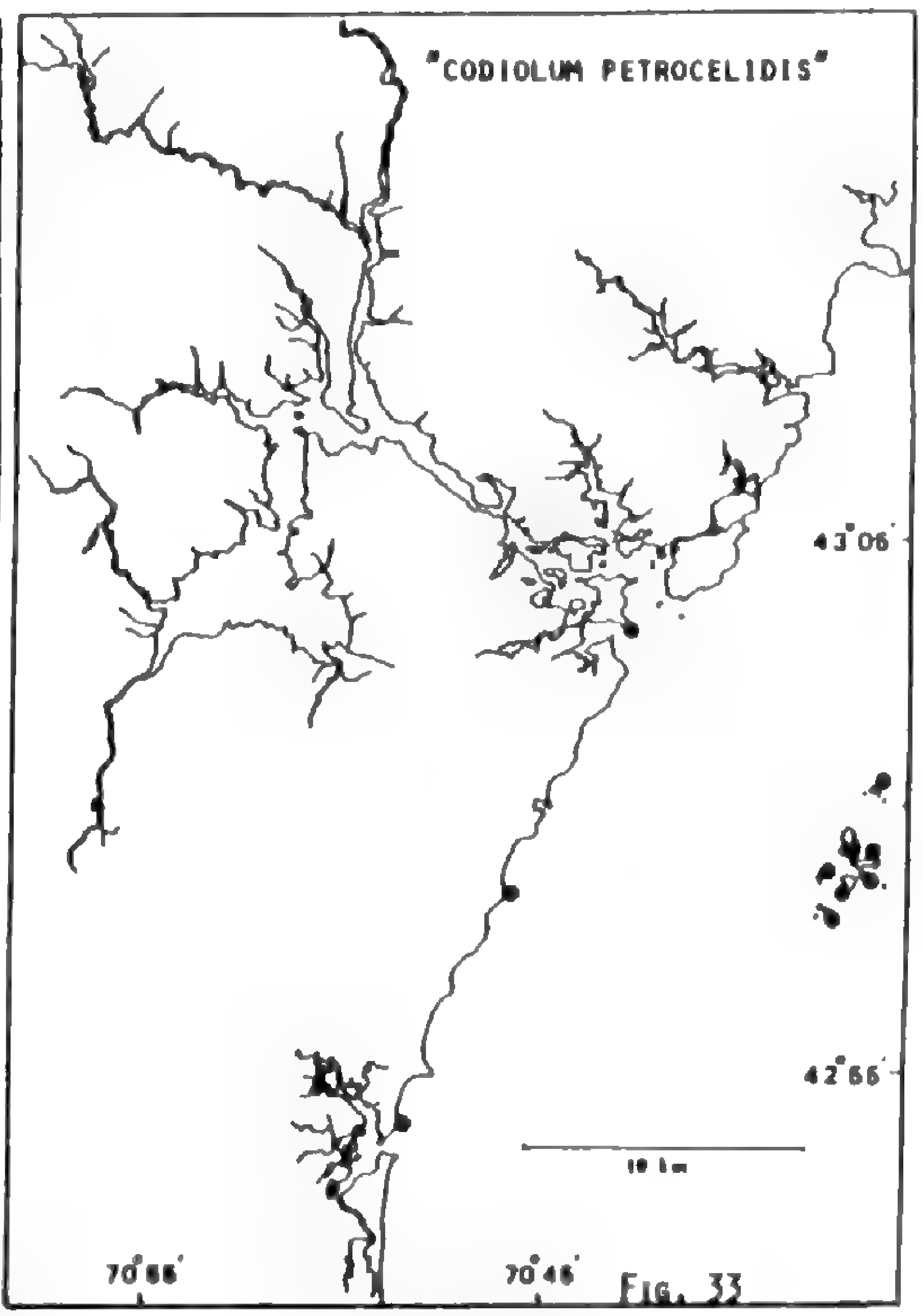


Fig. 33

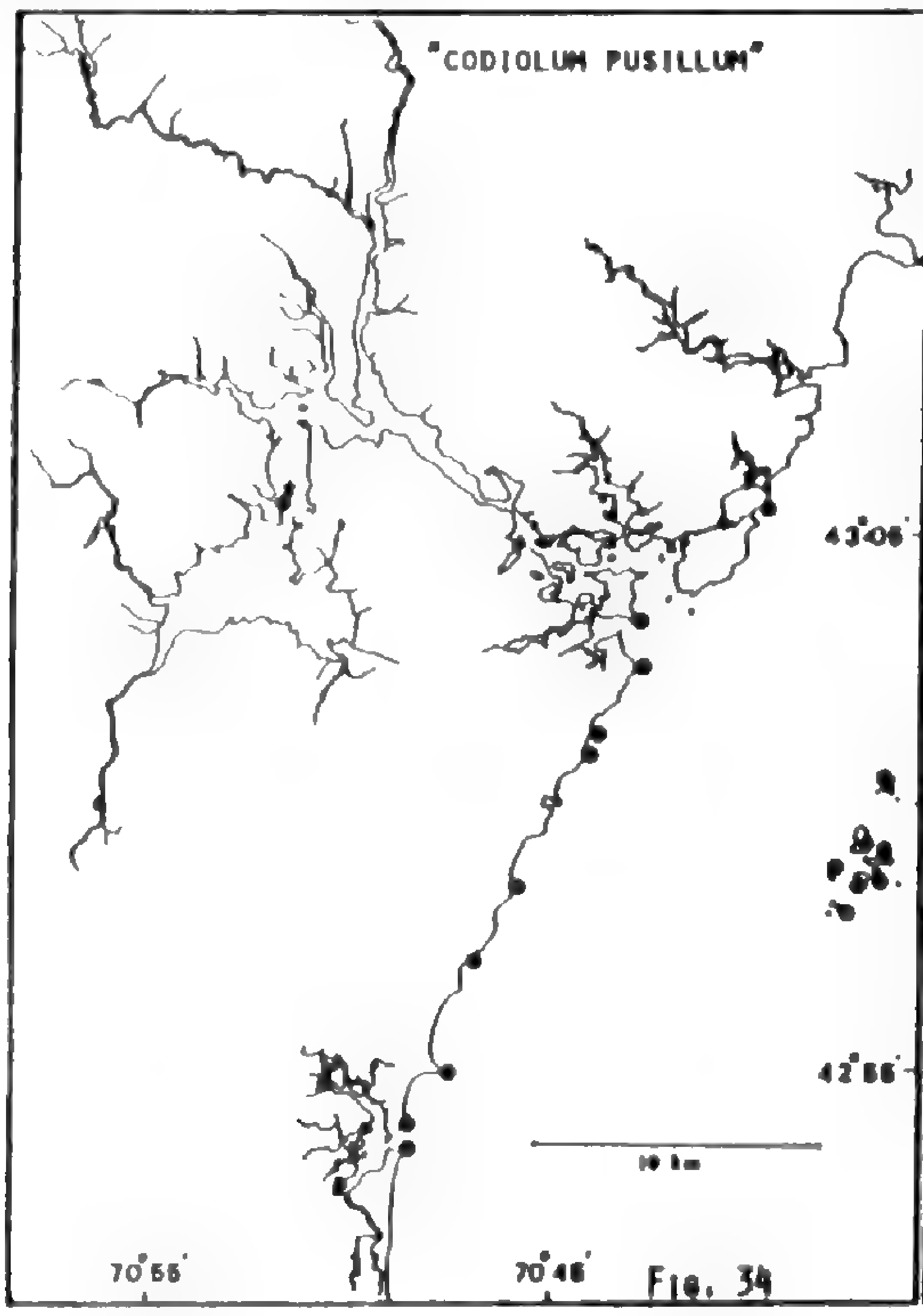


Fig. 34

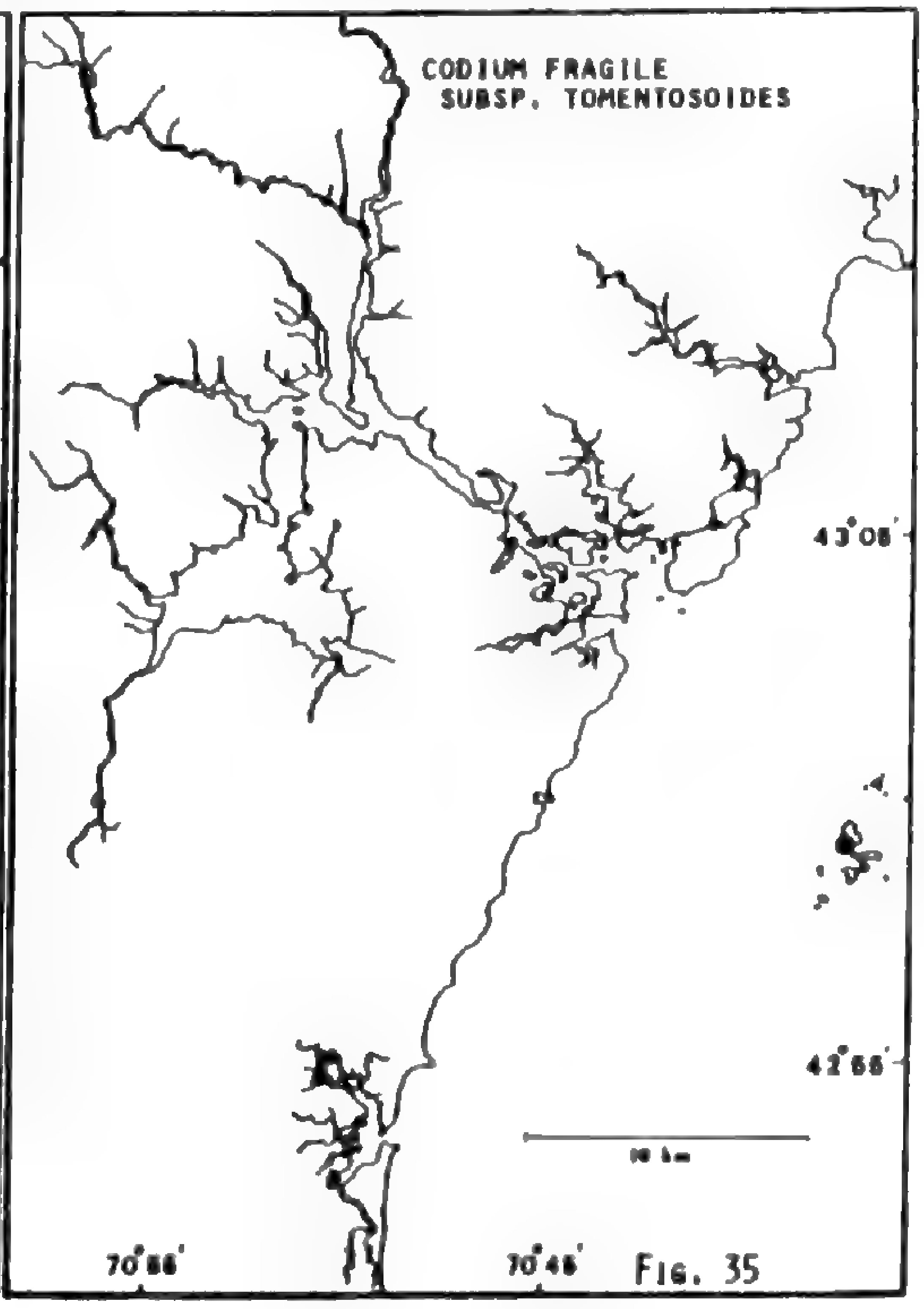


Fig. 35

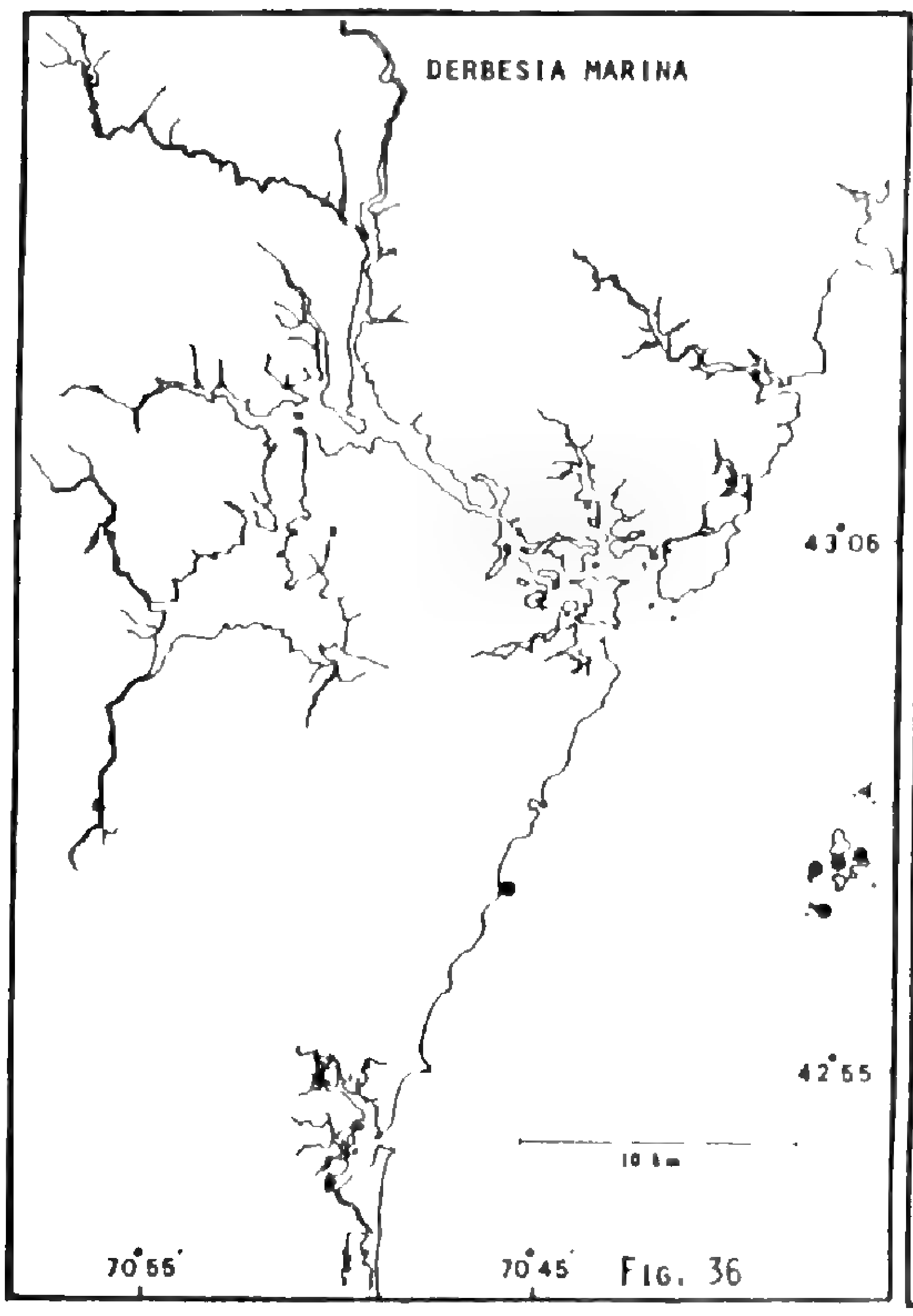


FIG. 36

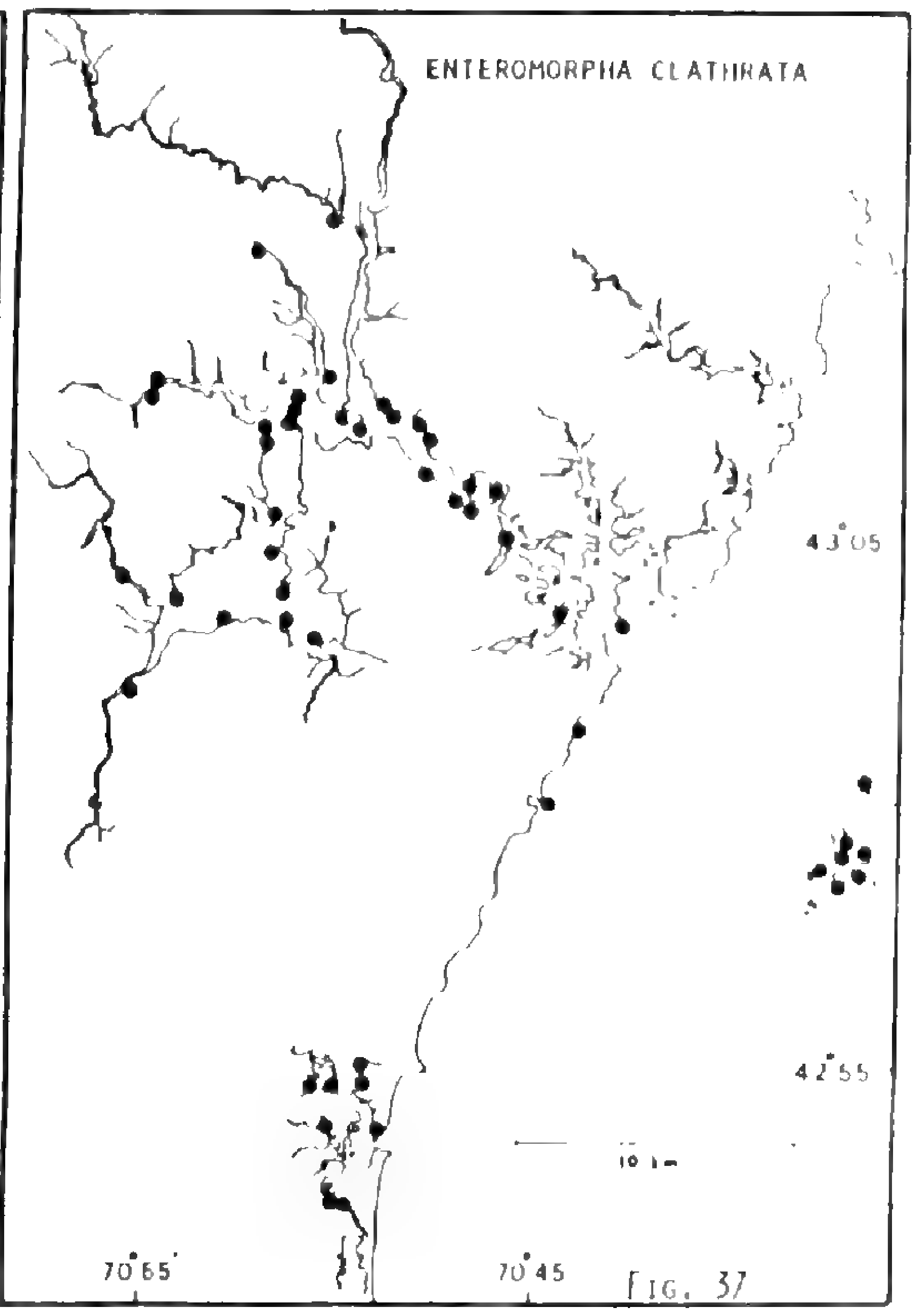


FIG. 37

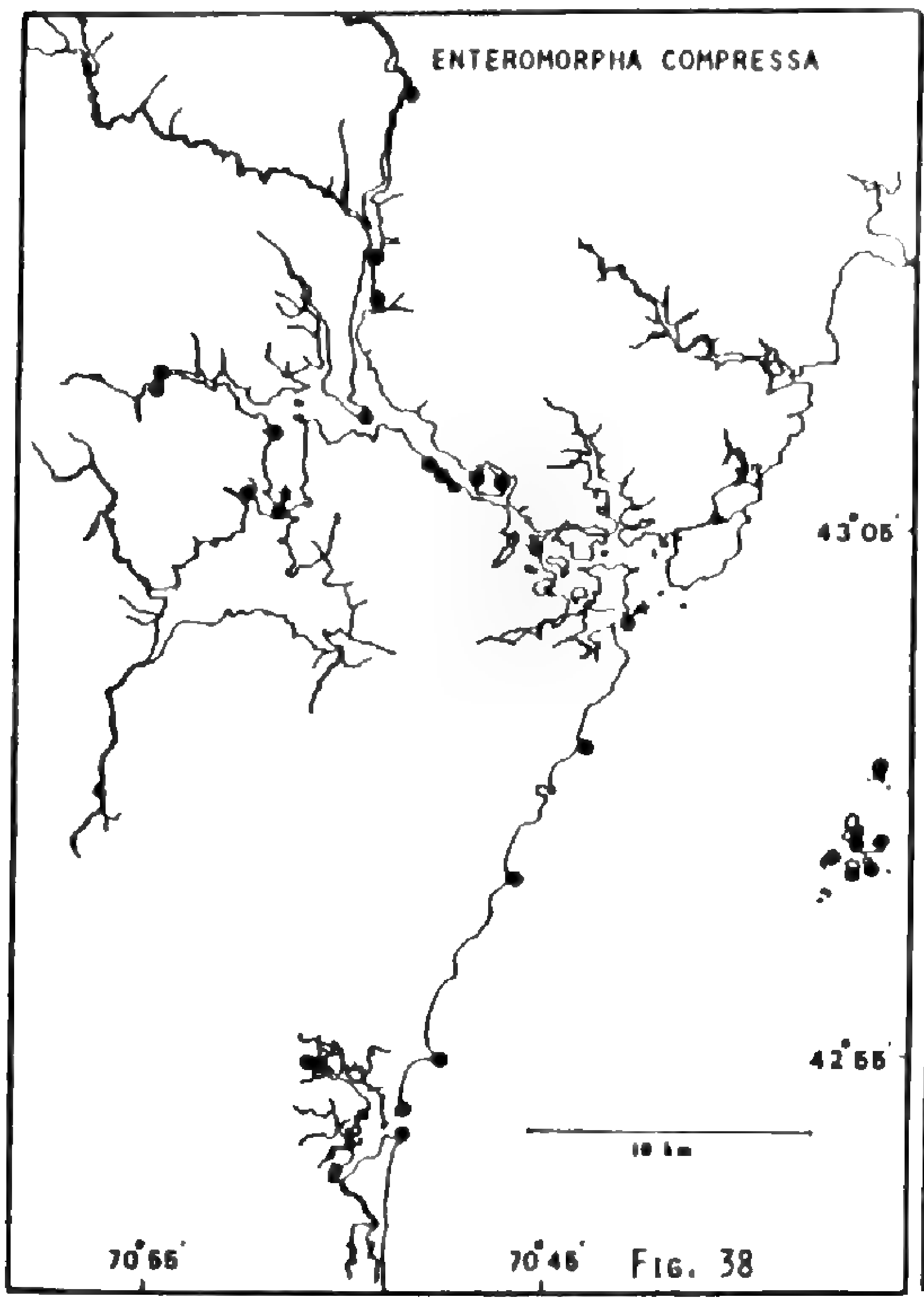


FIG. 38

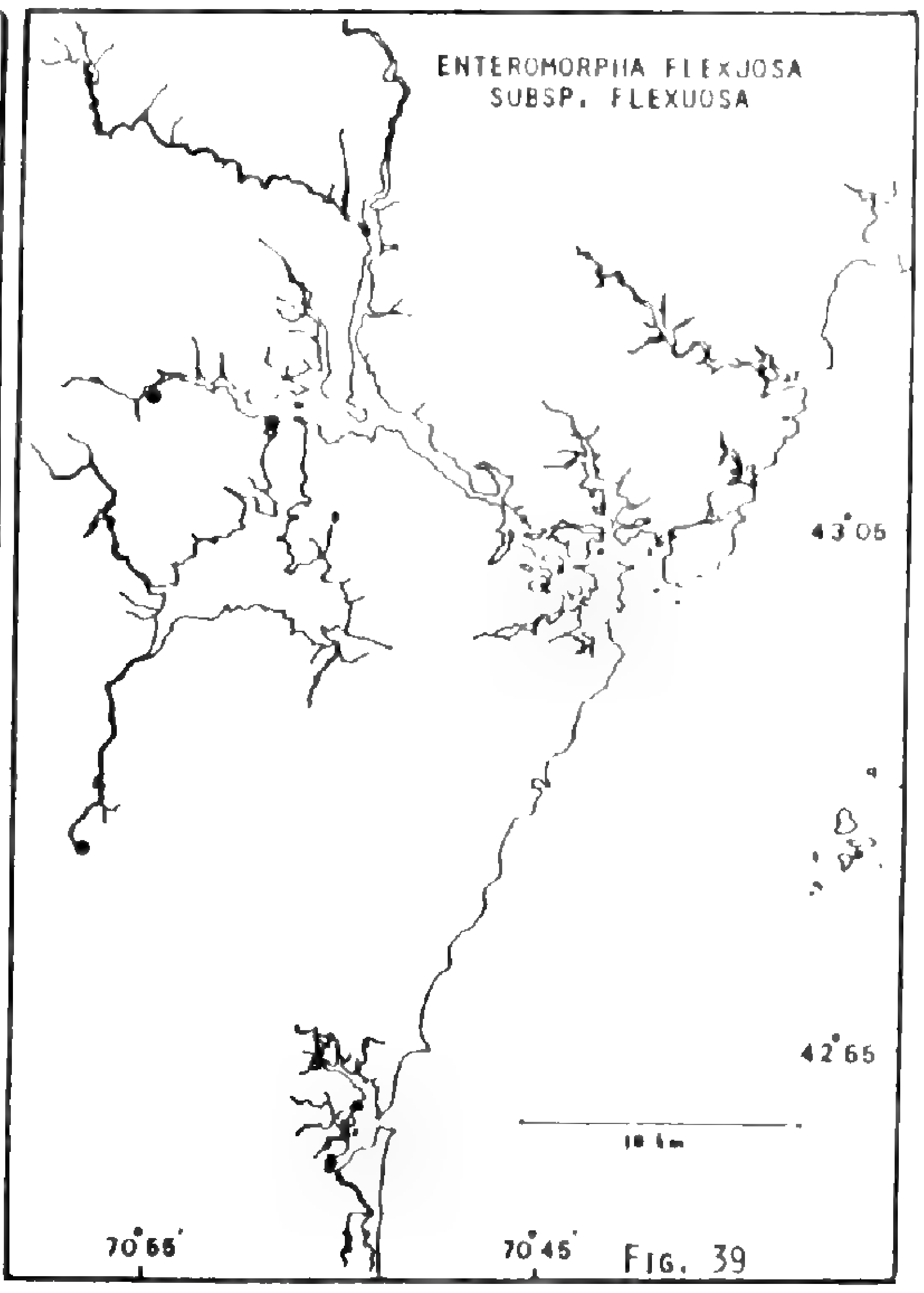


FIG. 39

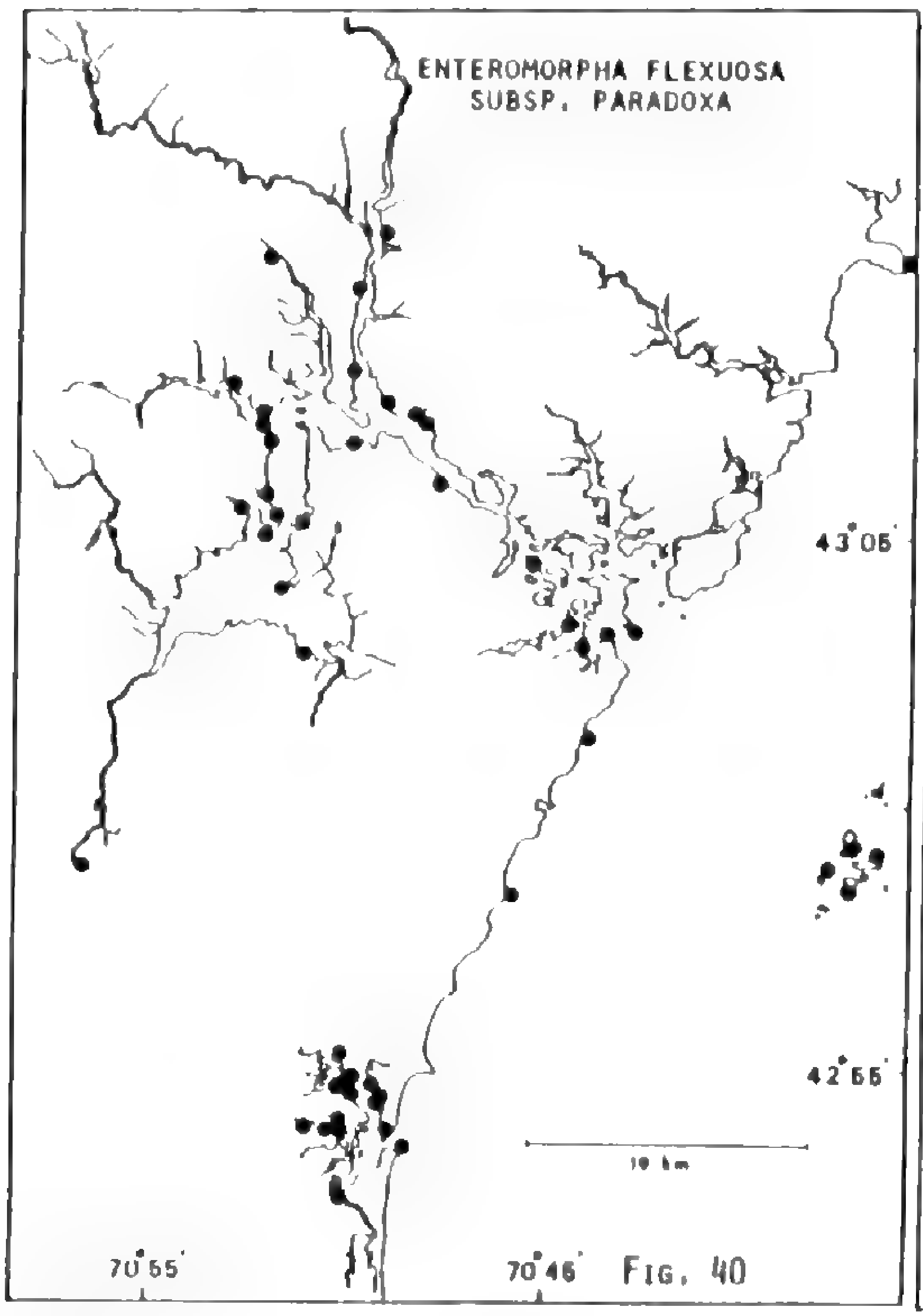


Fig. 40

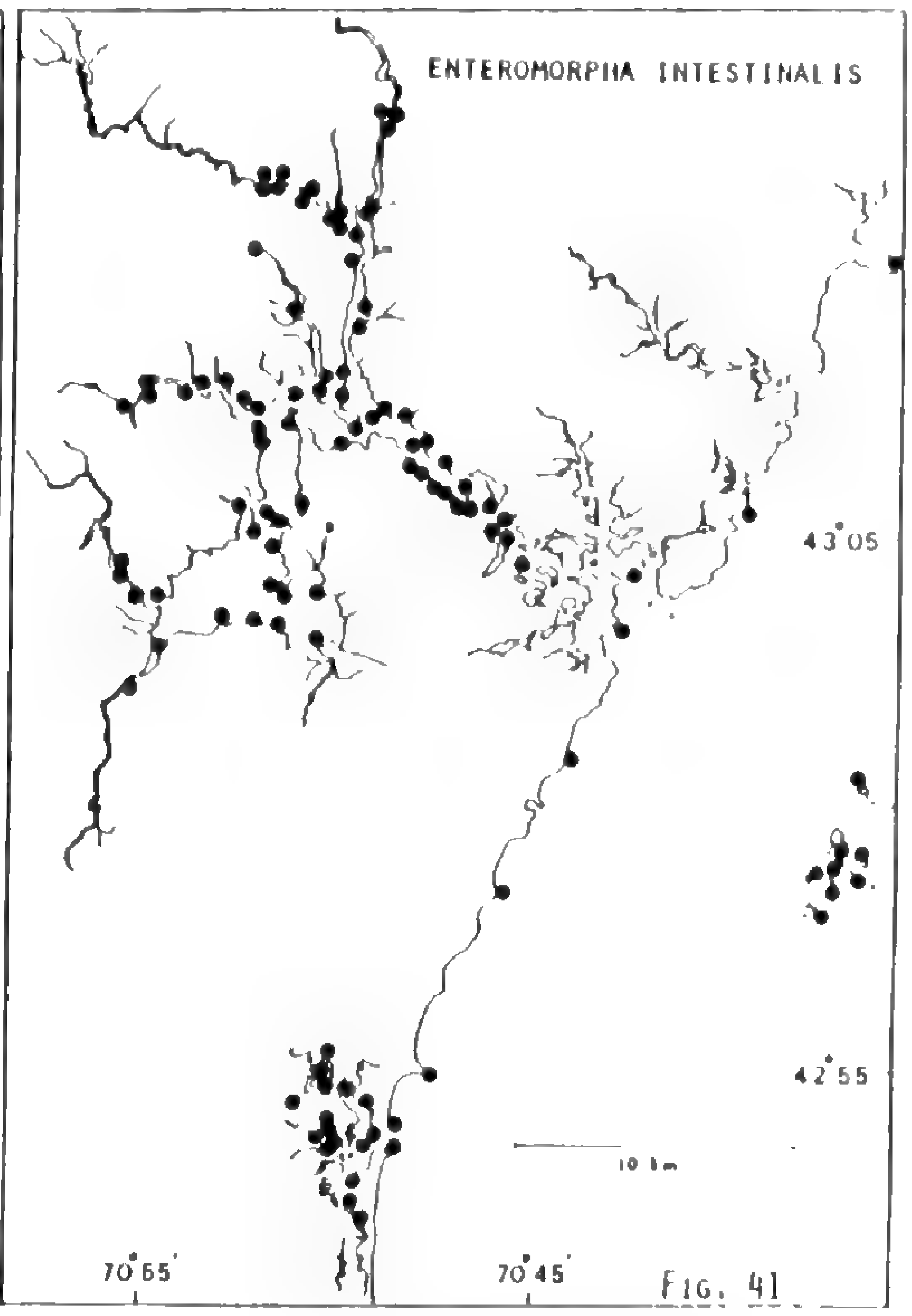


Fig. 41

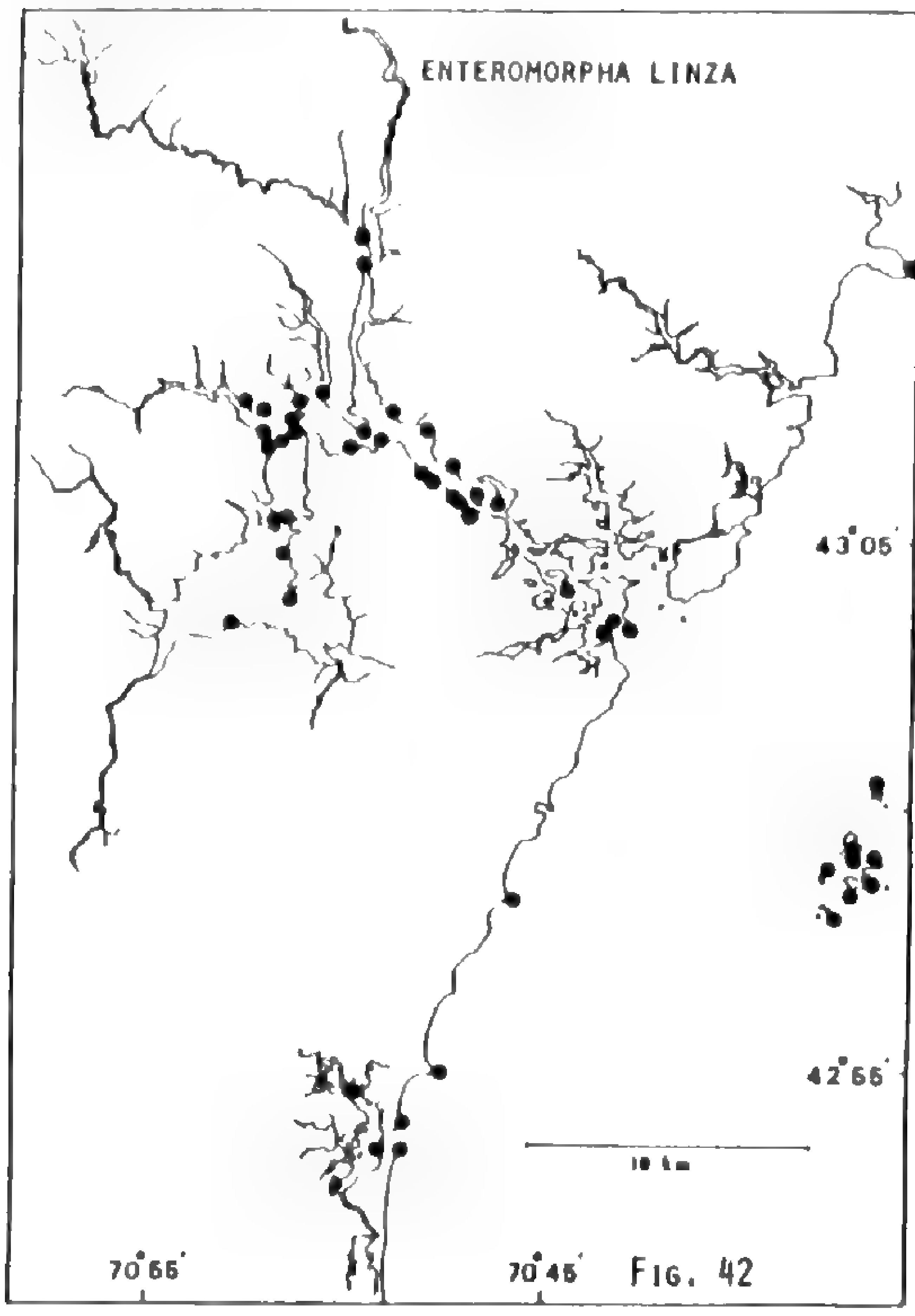


Fig. 42

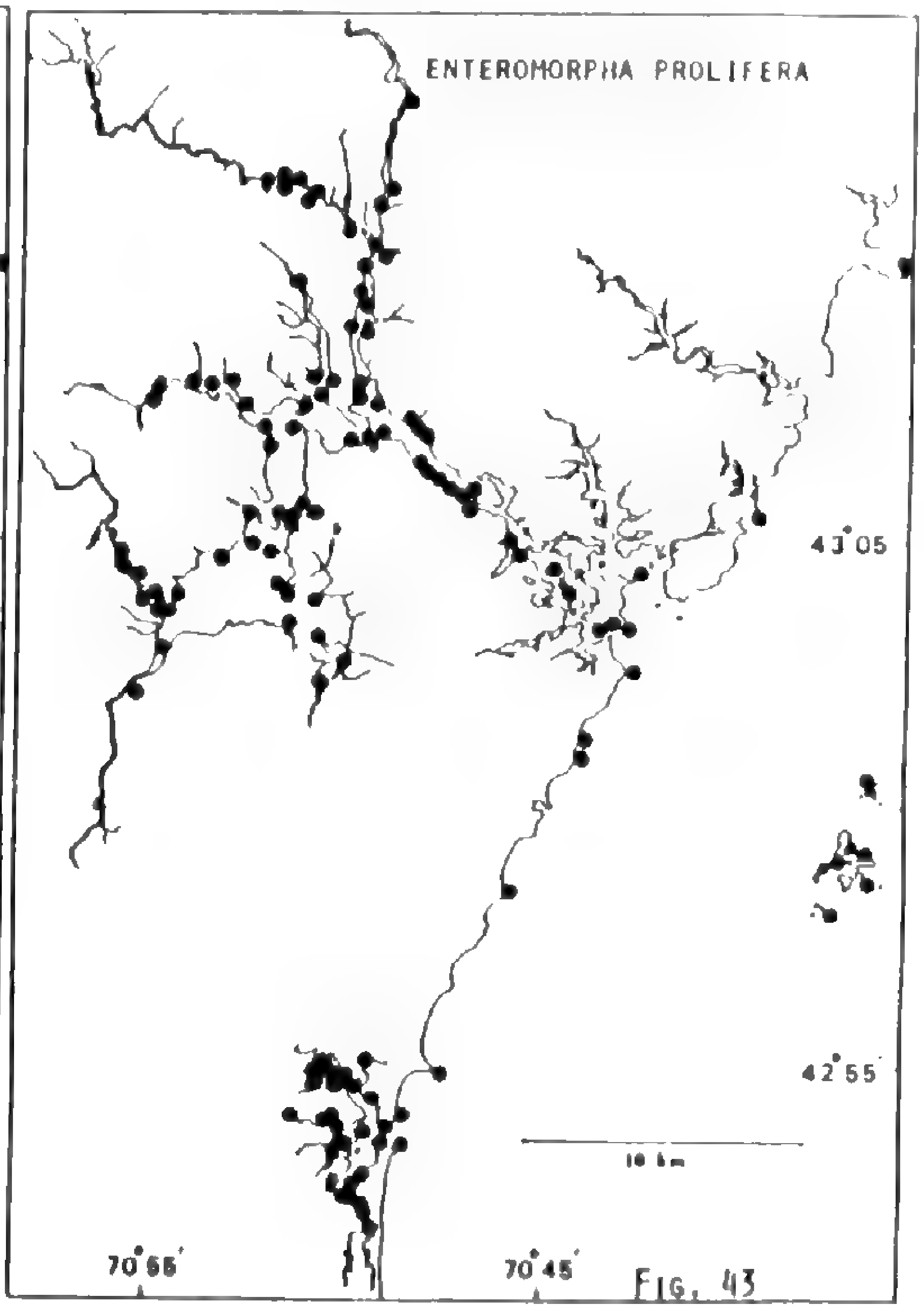


Fig. 43

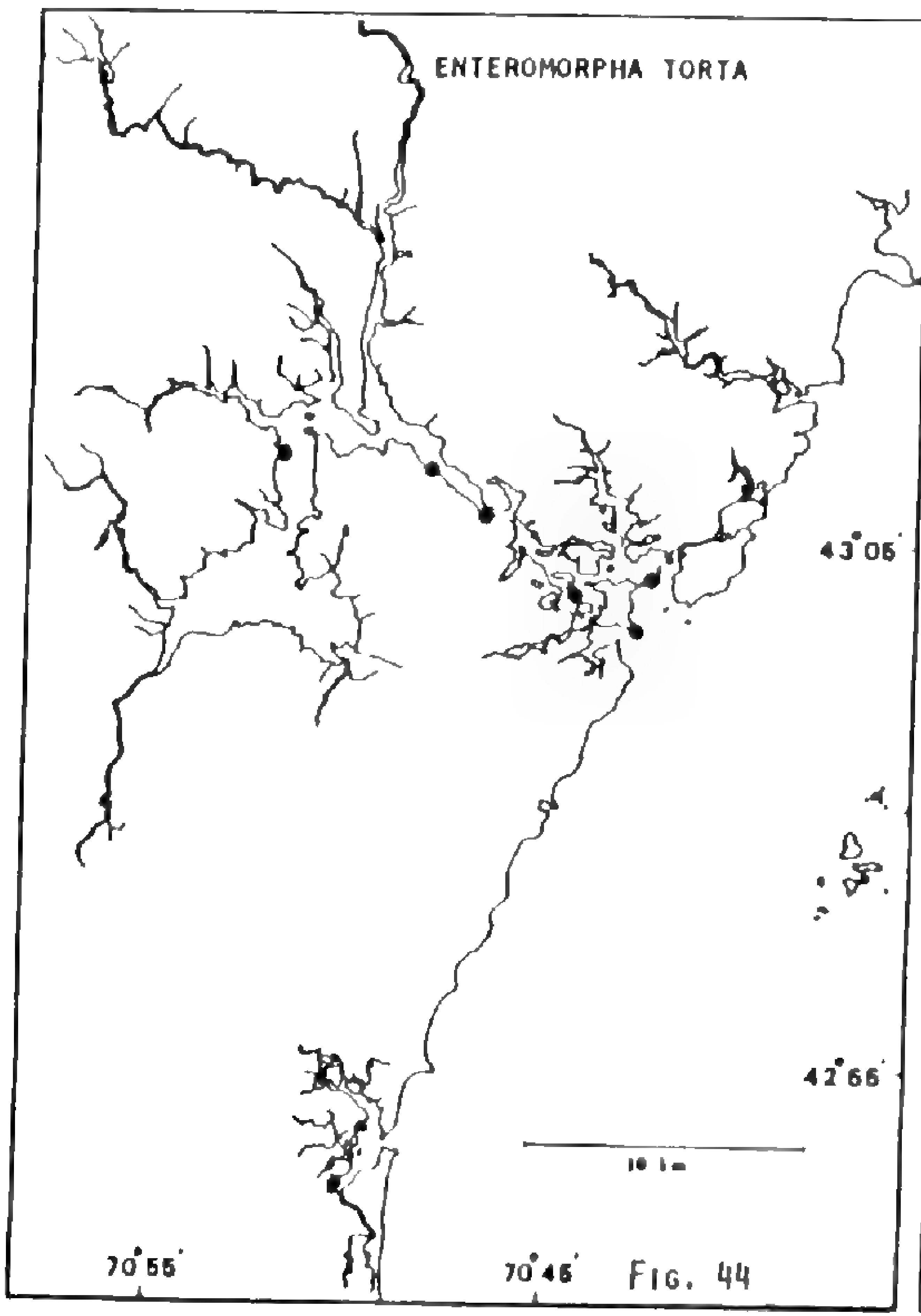


Fig. 44

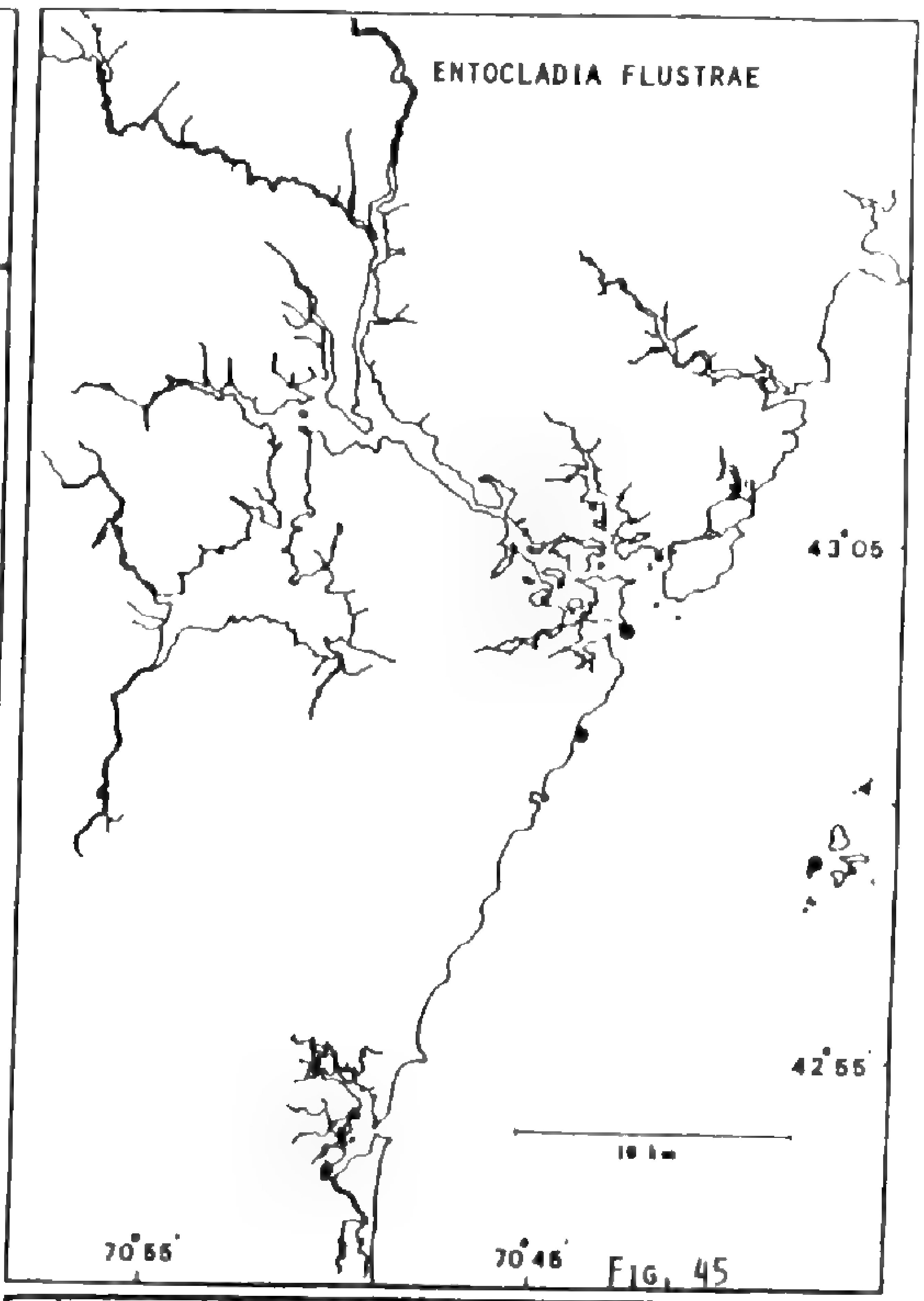


Fig. 45

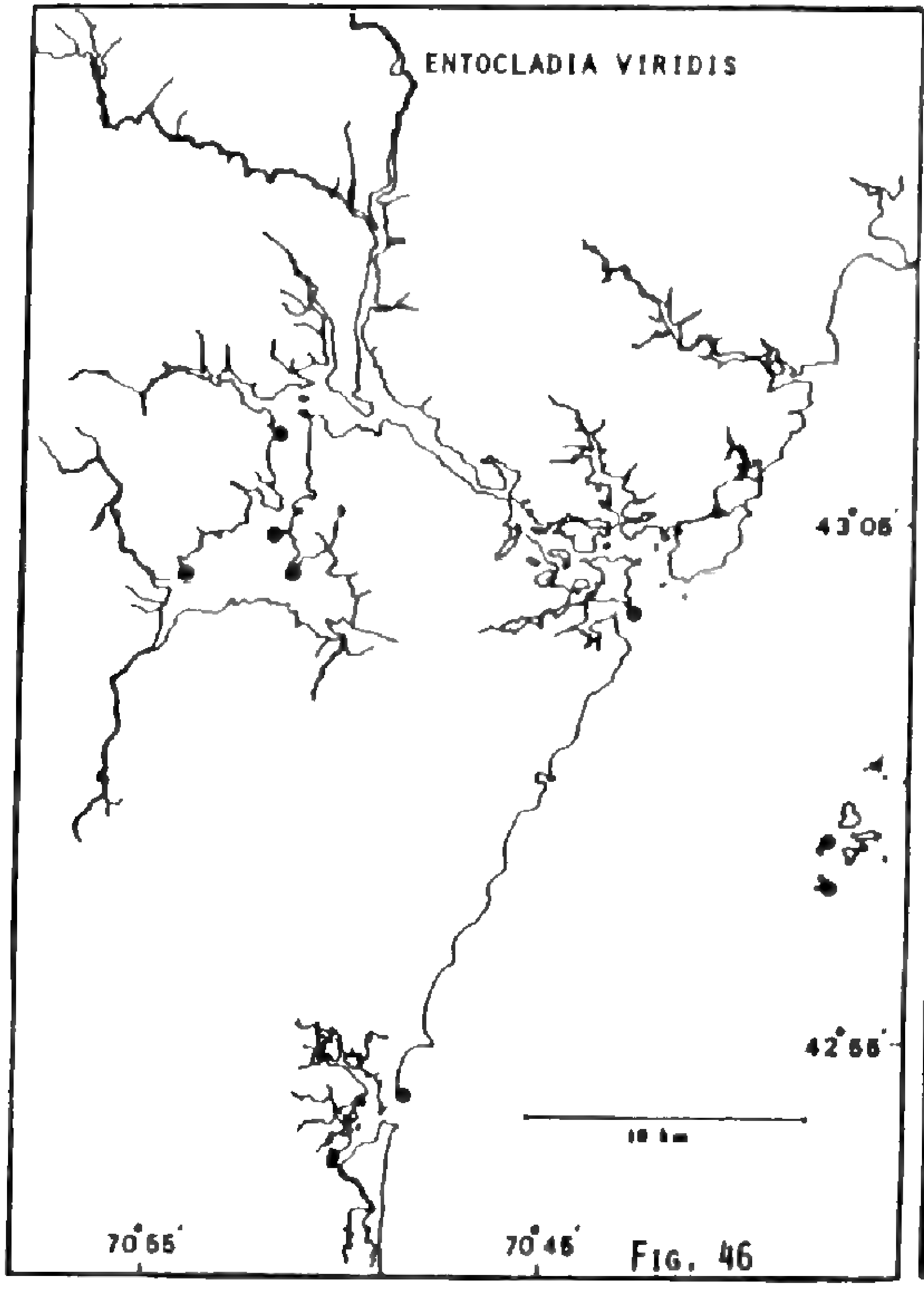


Fig. 46

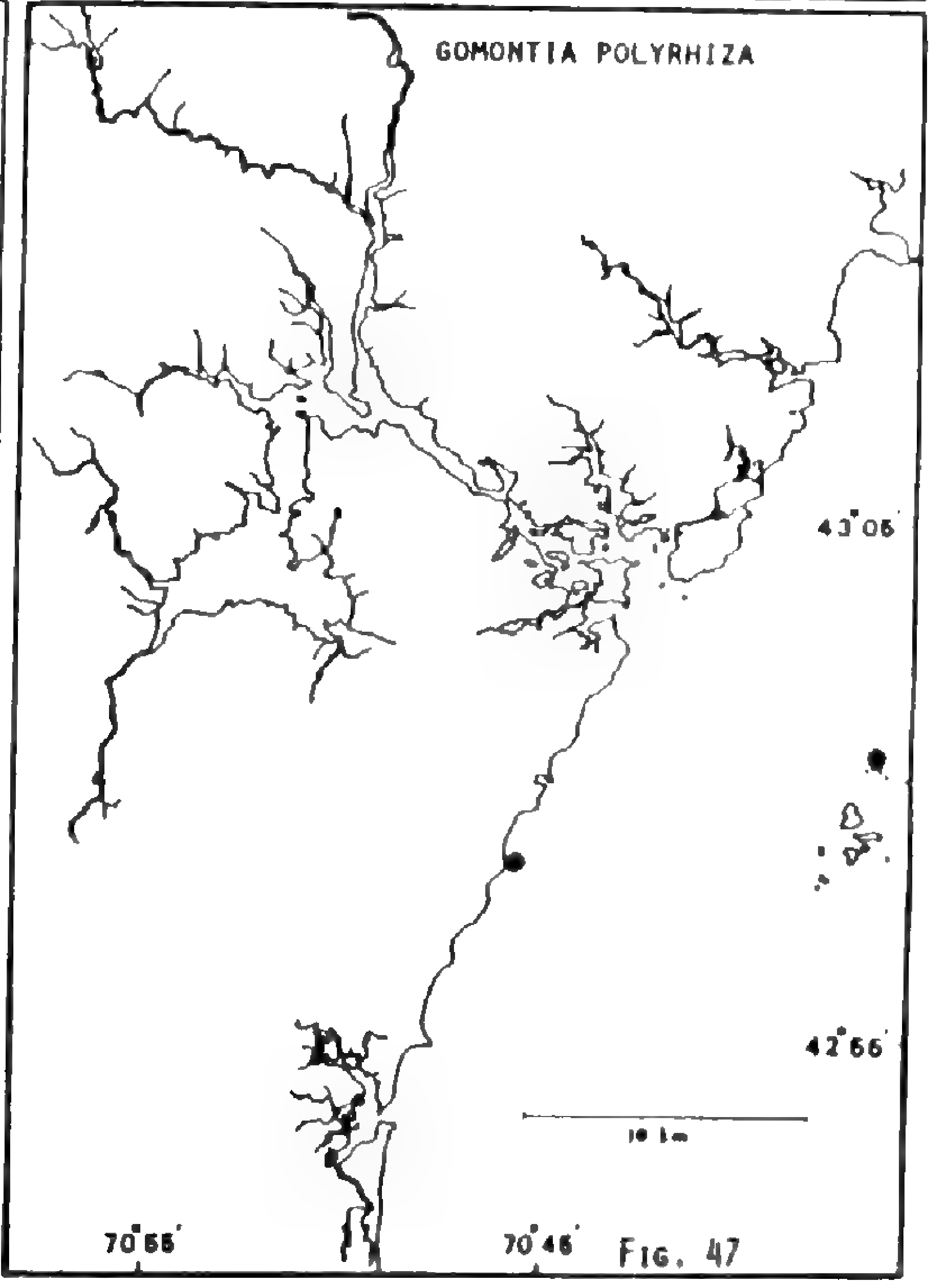


Fig. 47

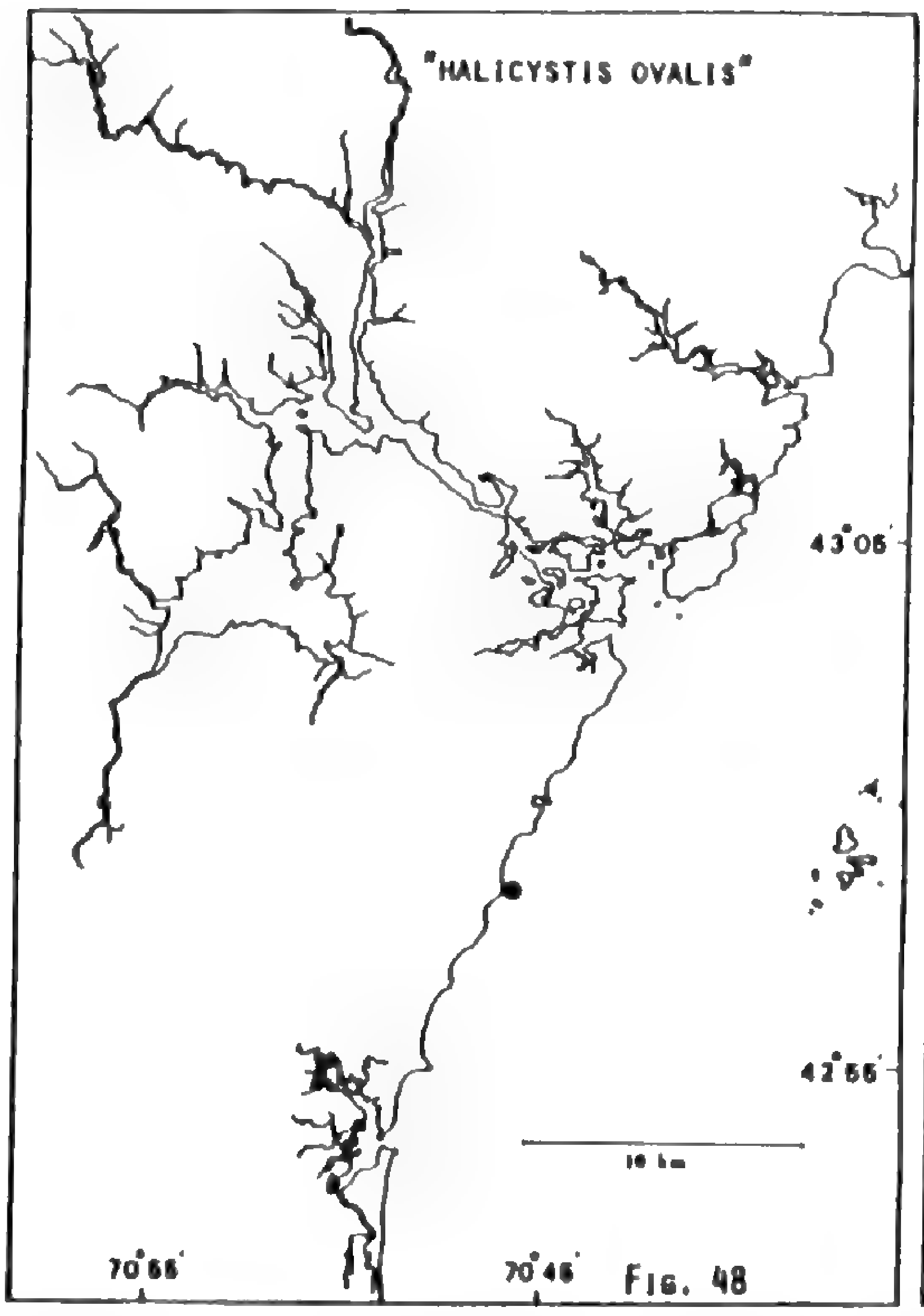


FIG. 48

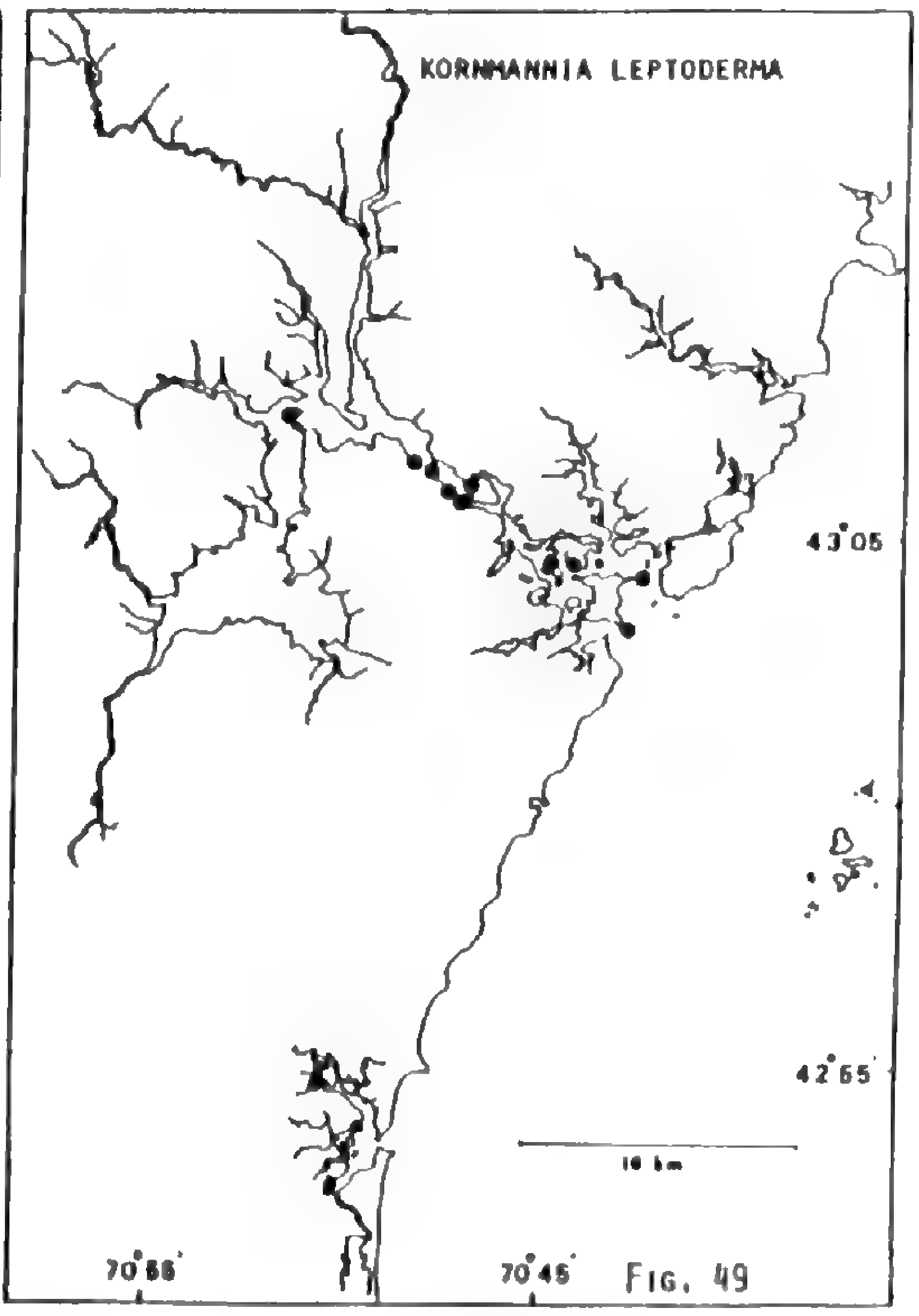


FIG. 49

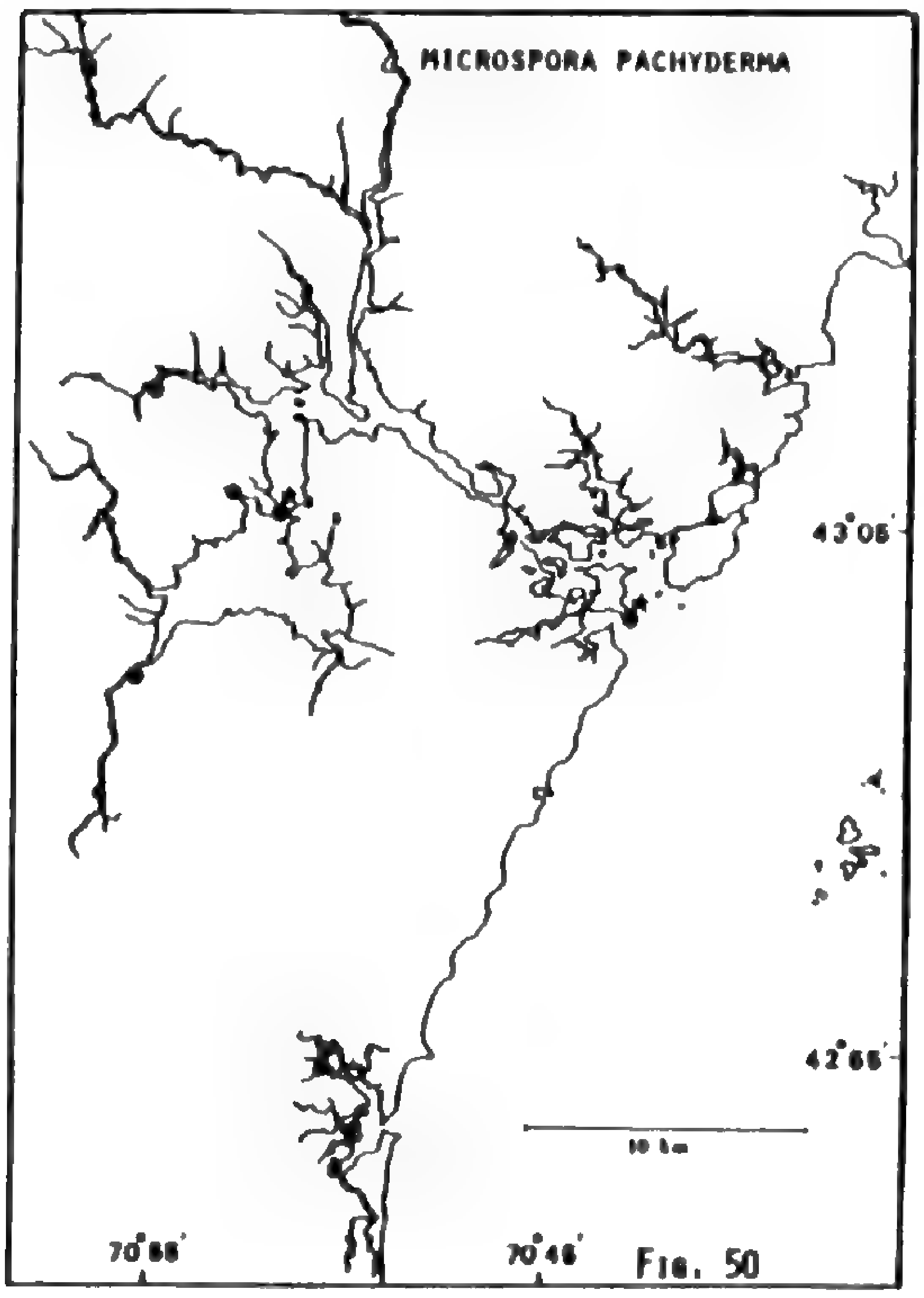


FIG. 50

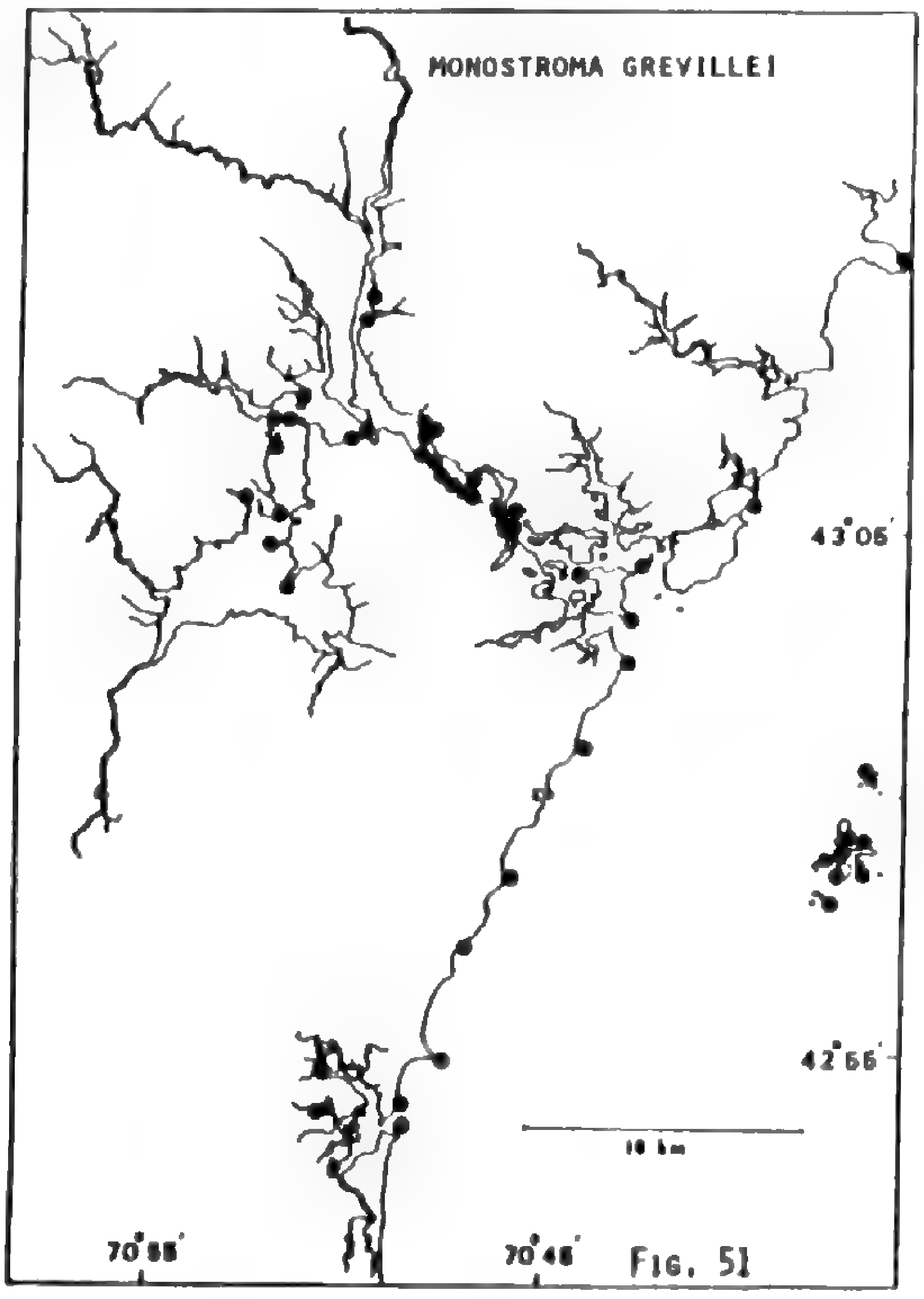


FIG. 51

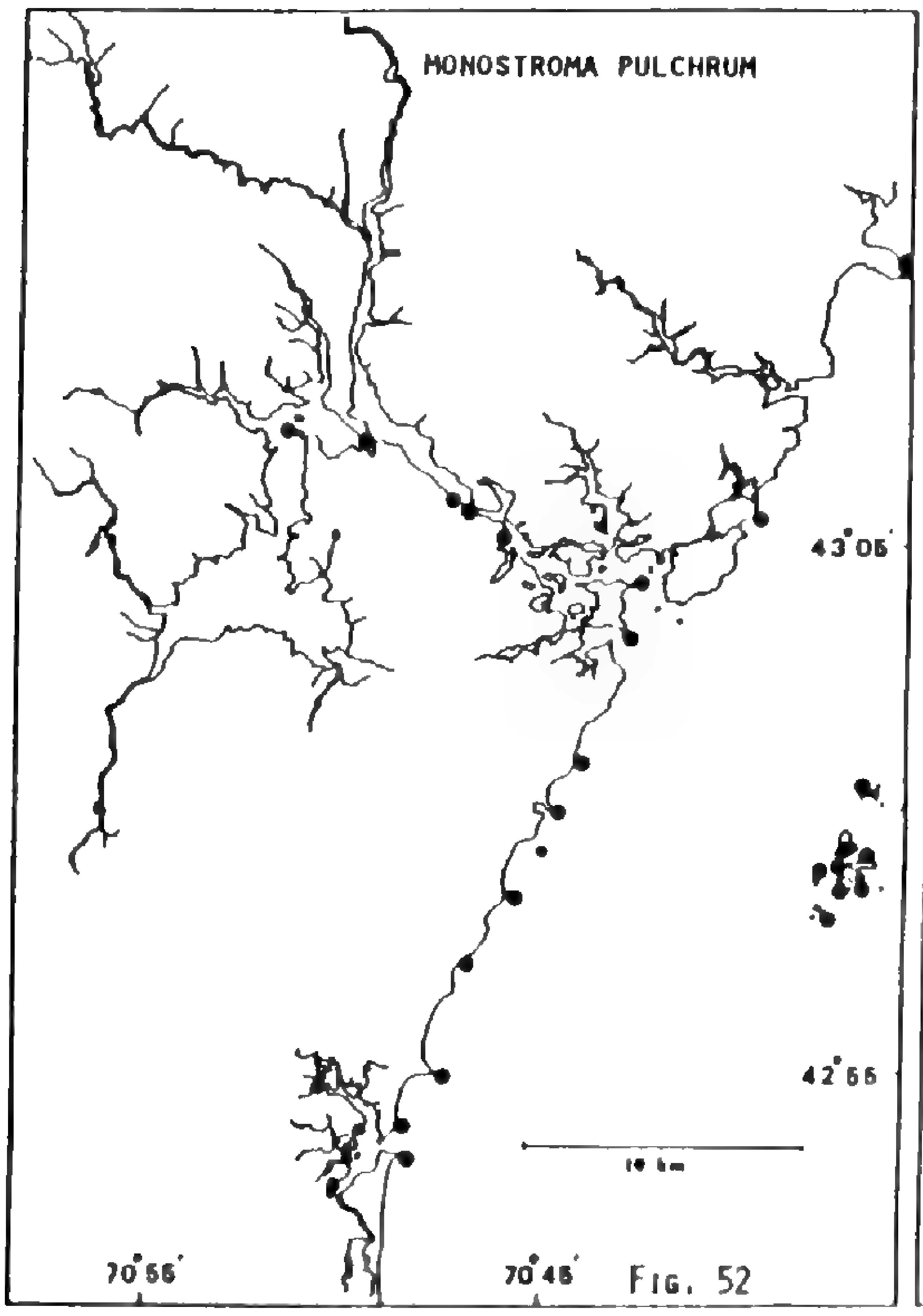
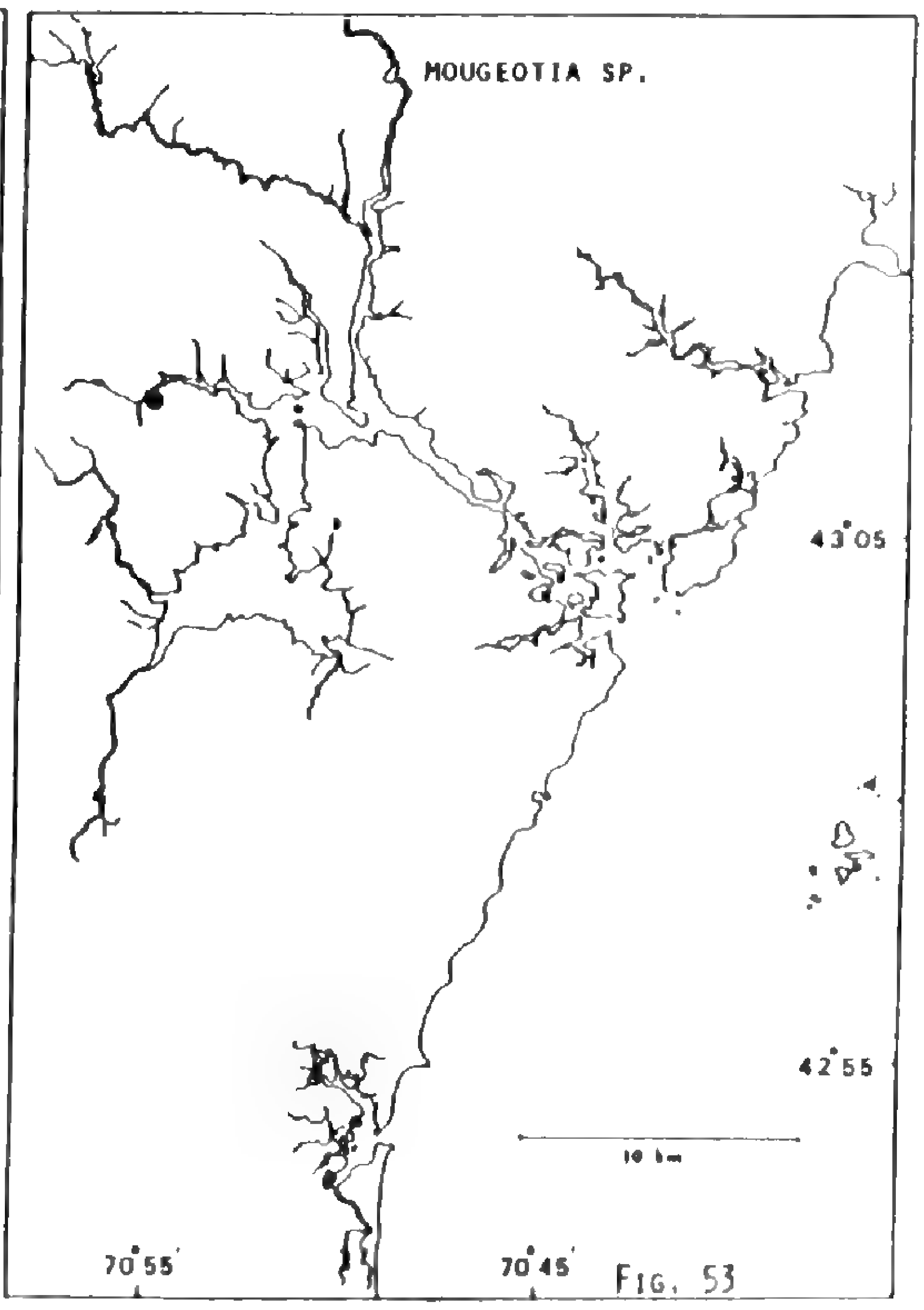


FIG. 52



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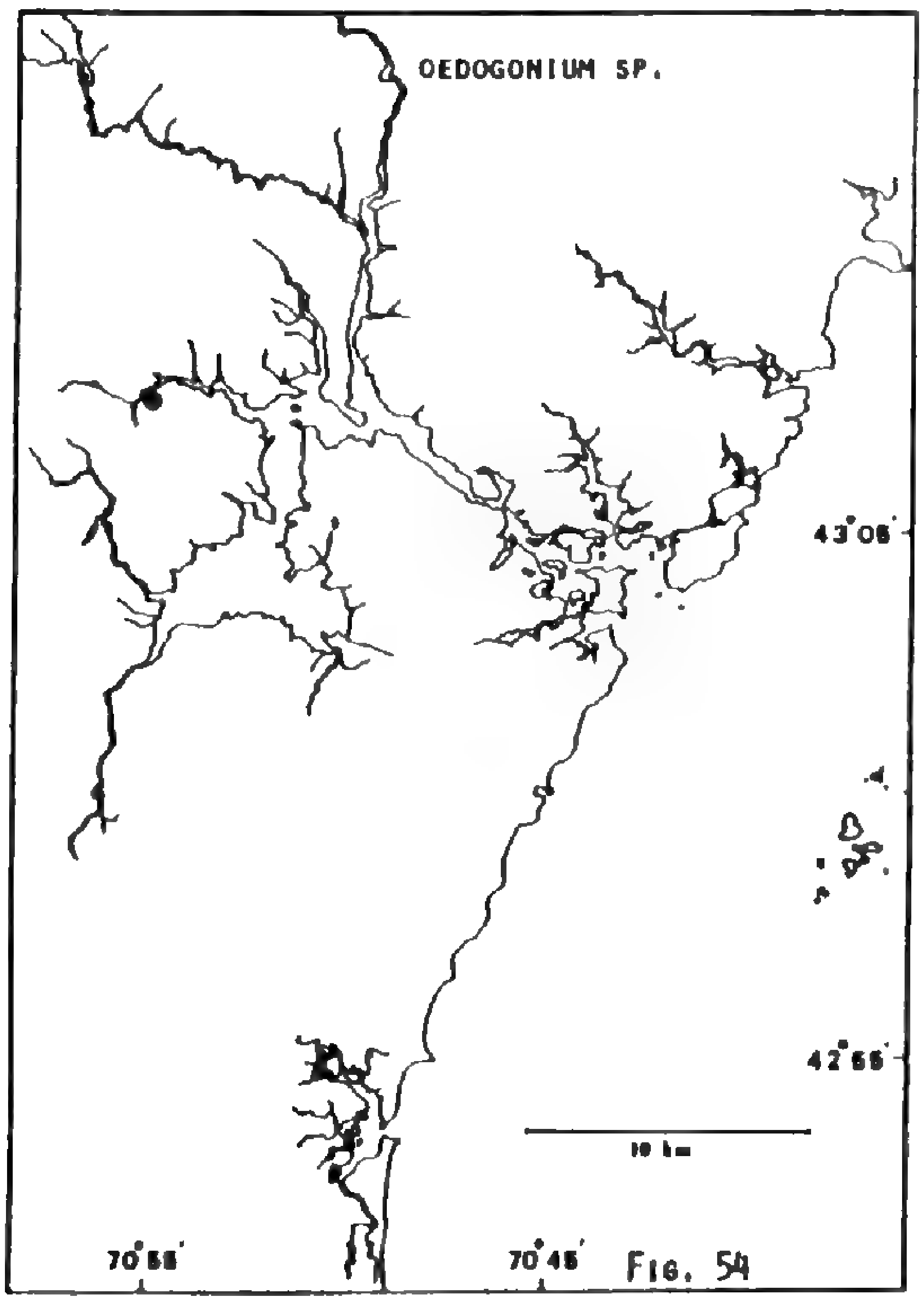


FIG. 54

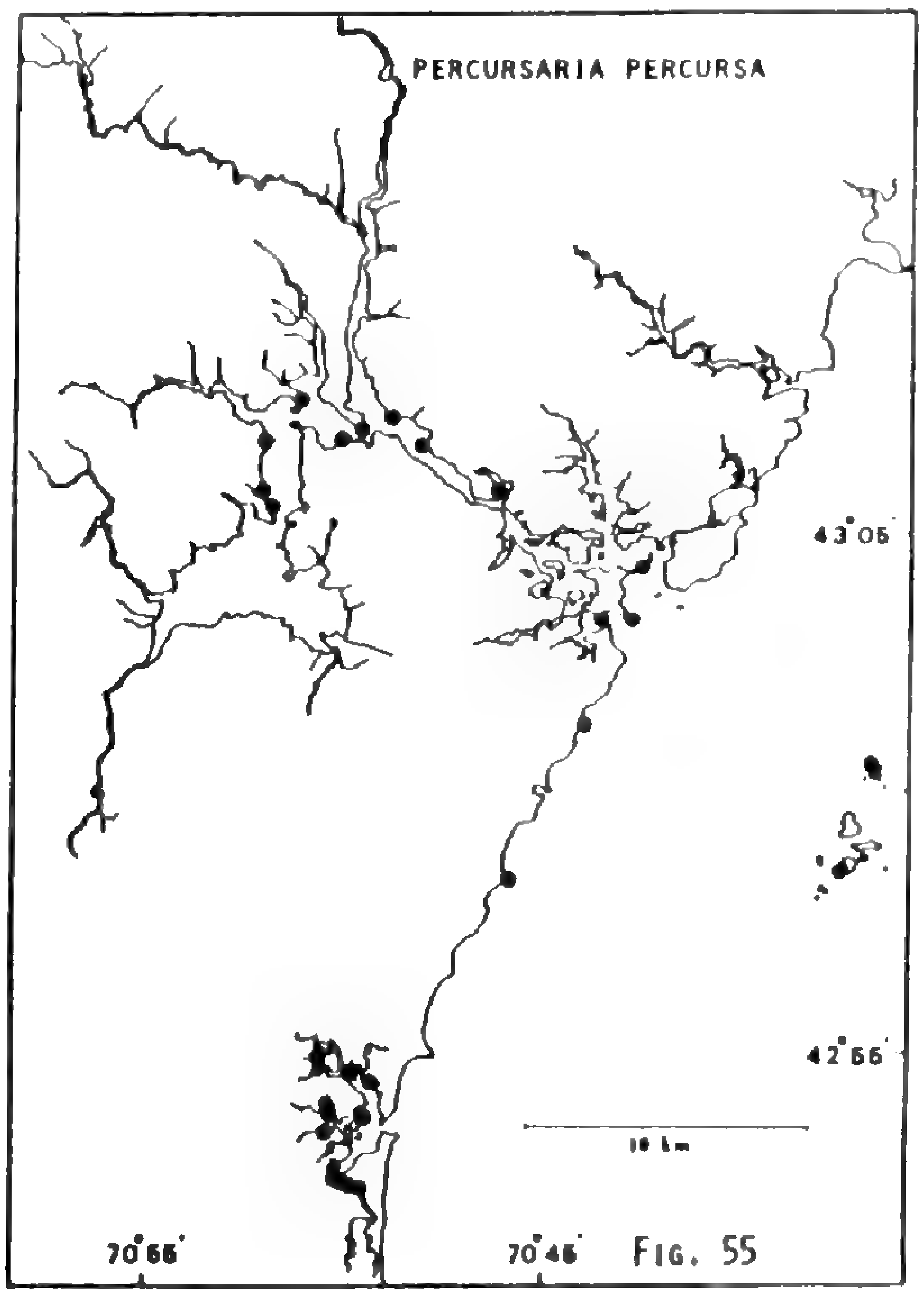


FIG. 55

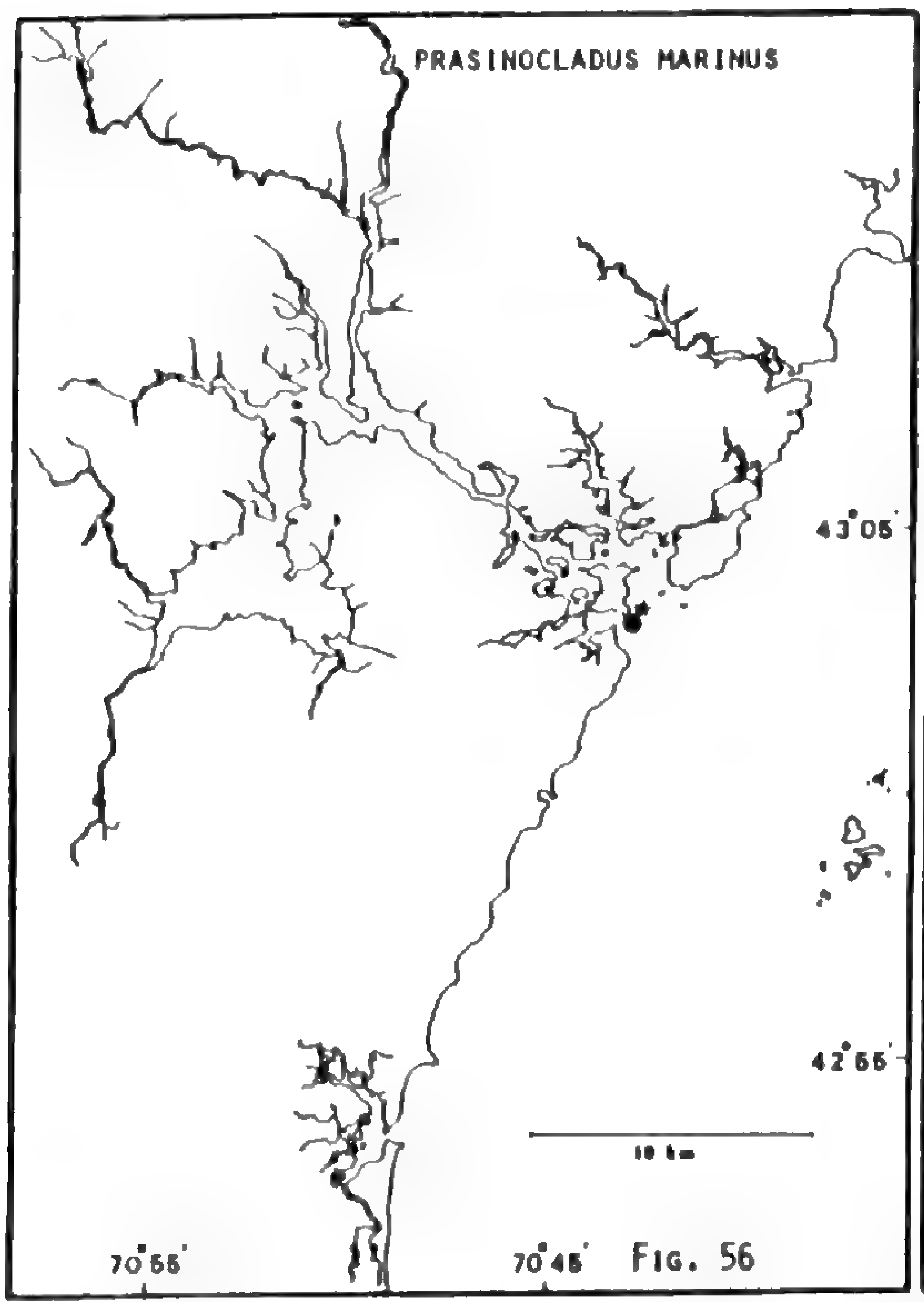


FIG. 56

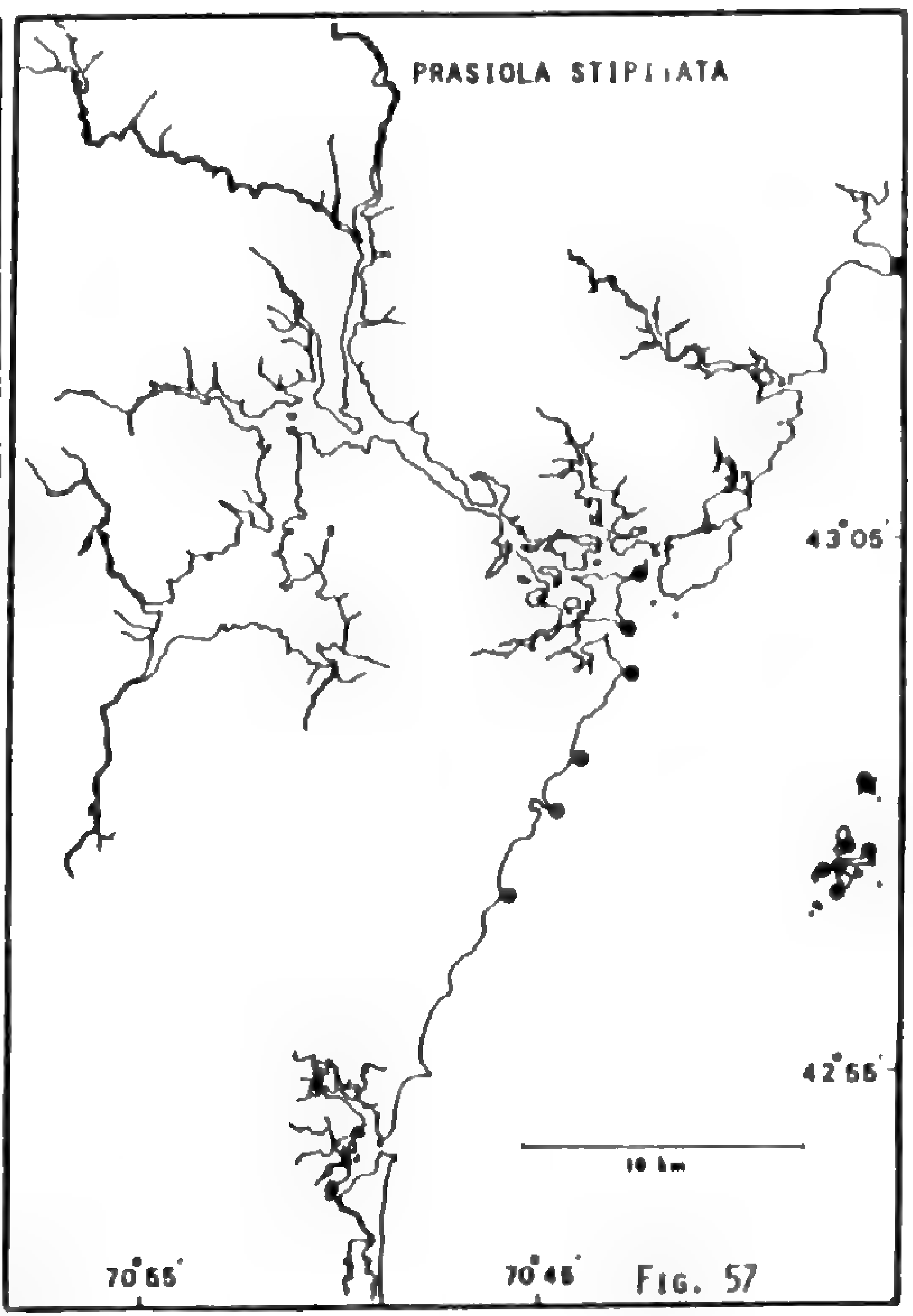


FIG. 57

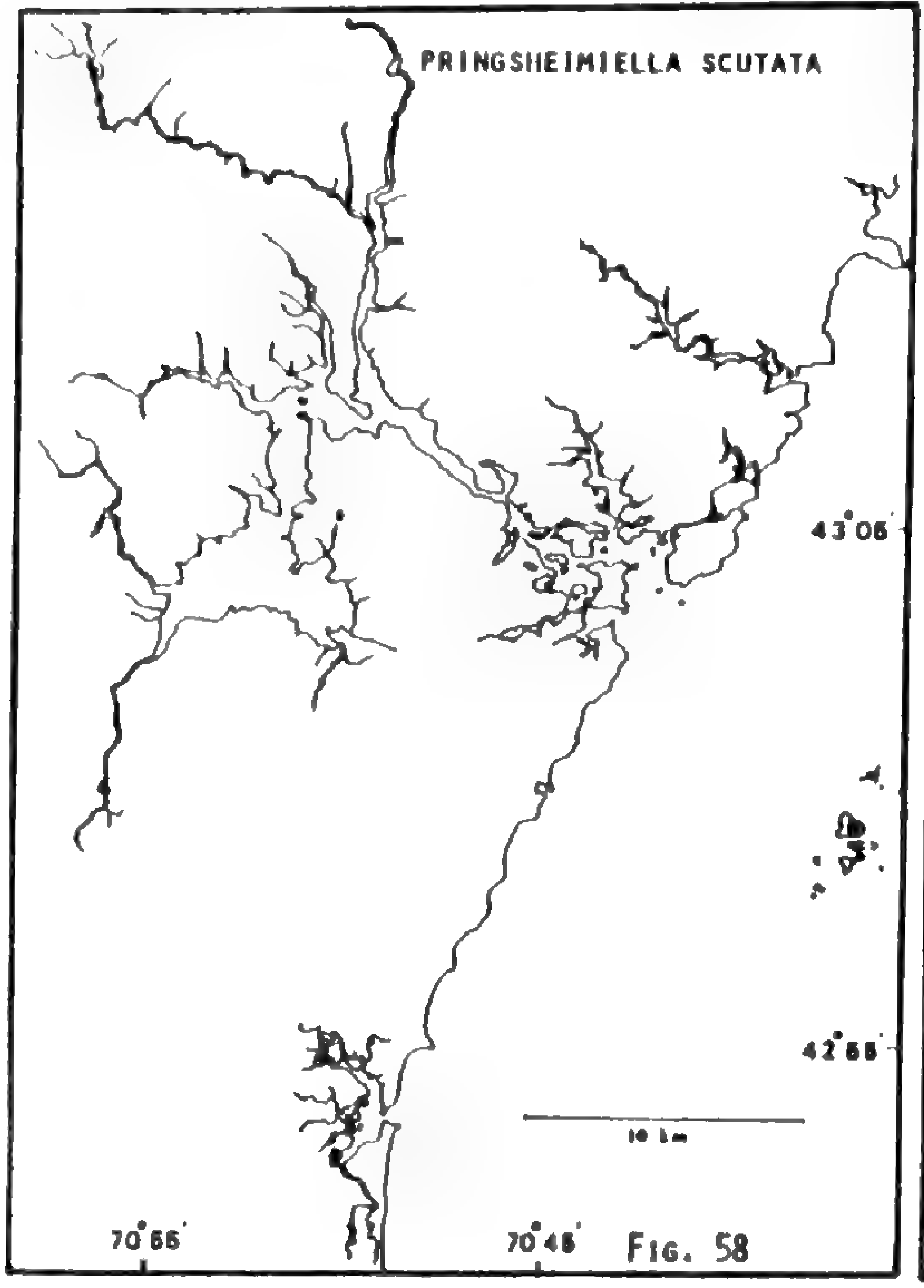


FIG. 58

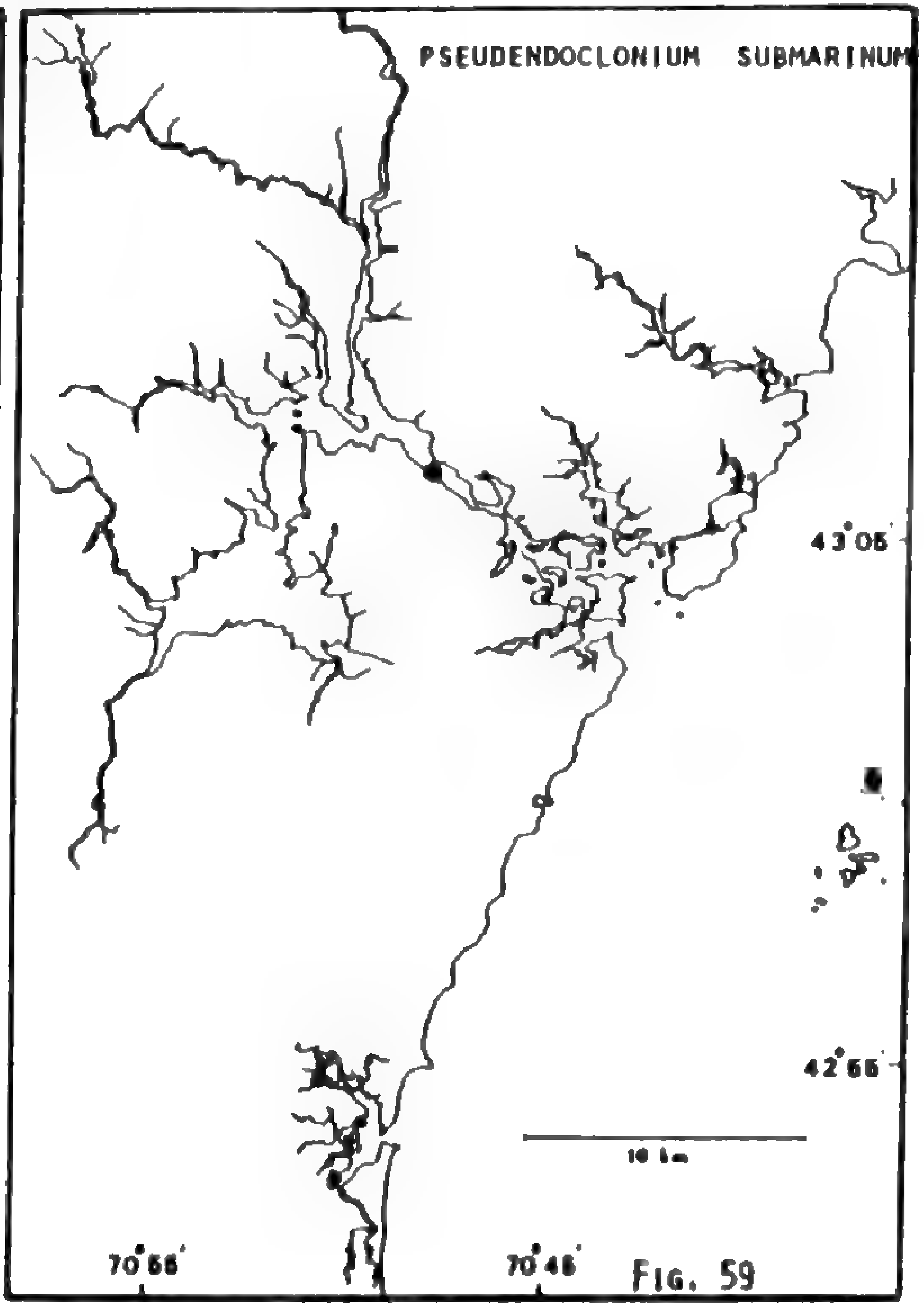


FIG. 59

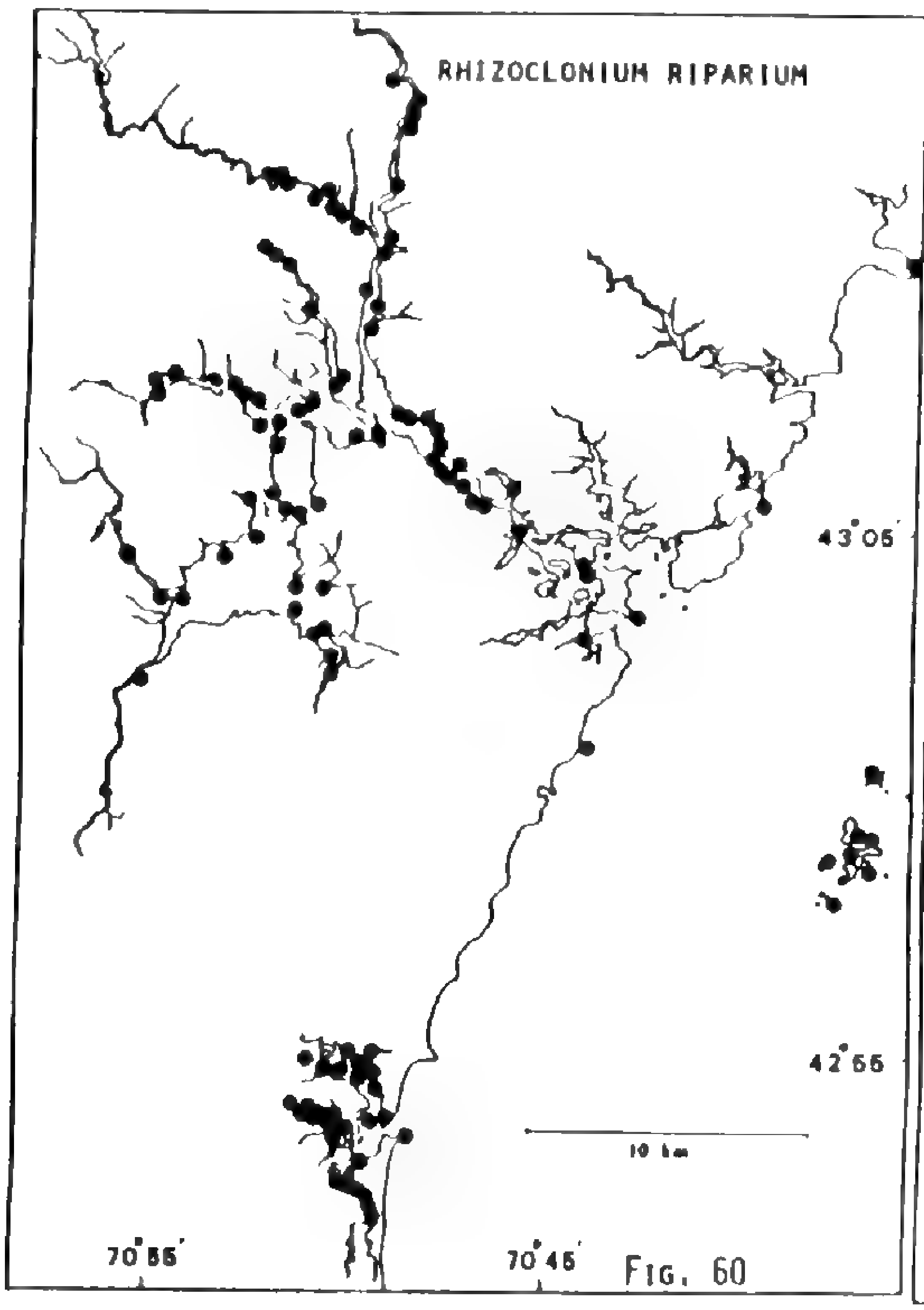


FIG. 60

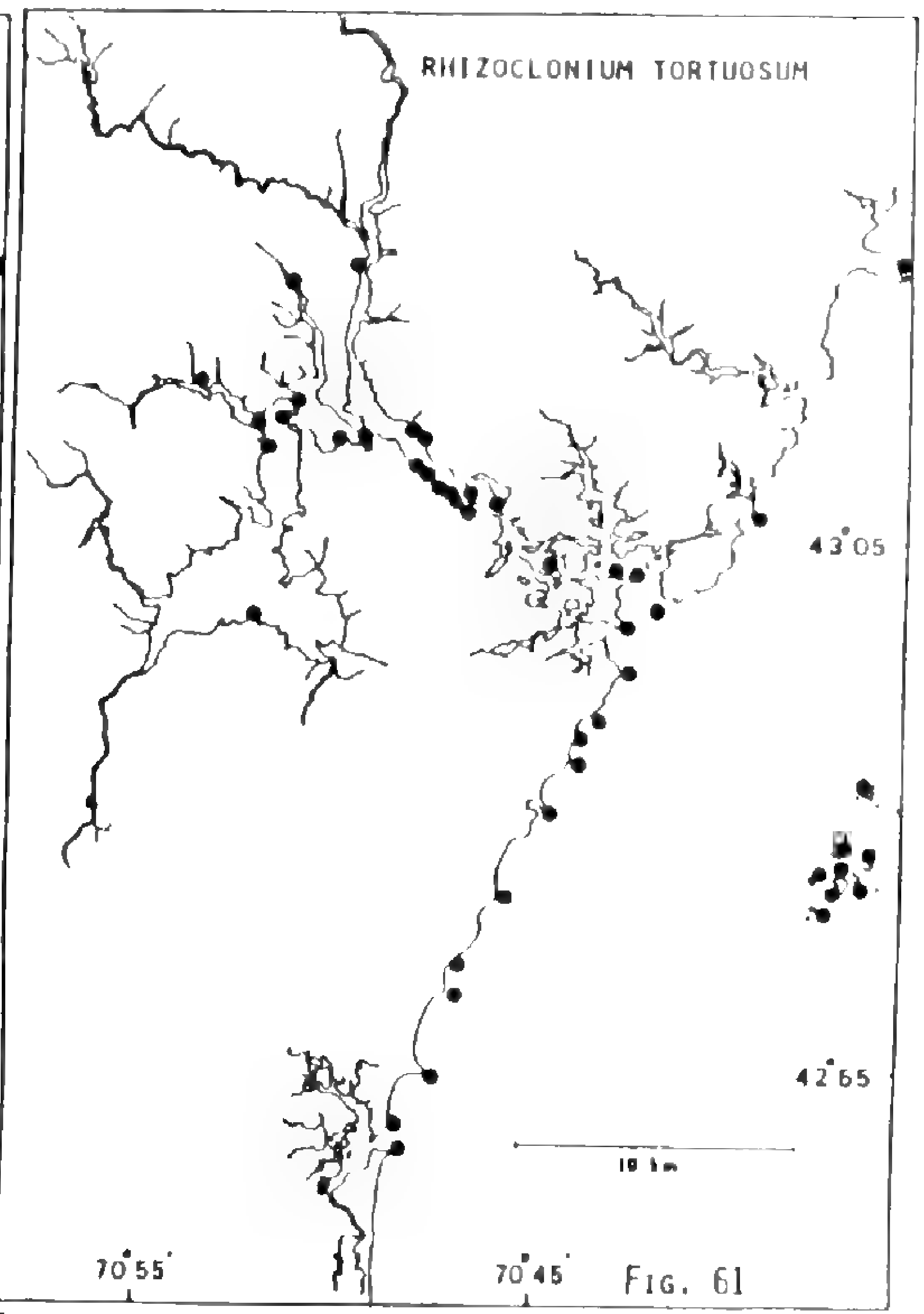


FIG. 61

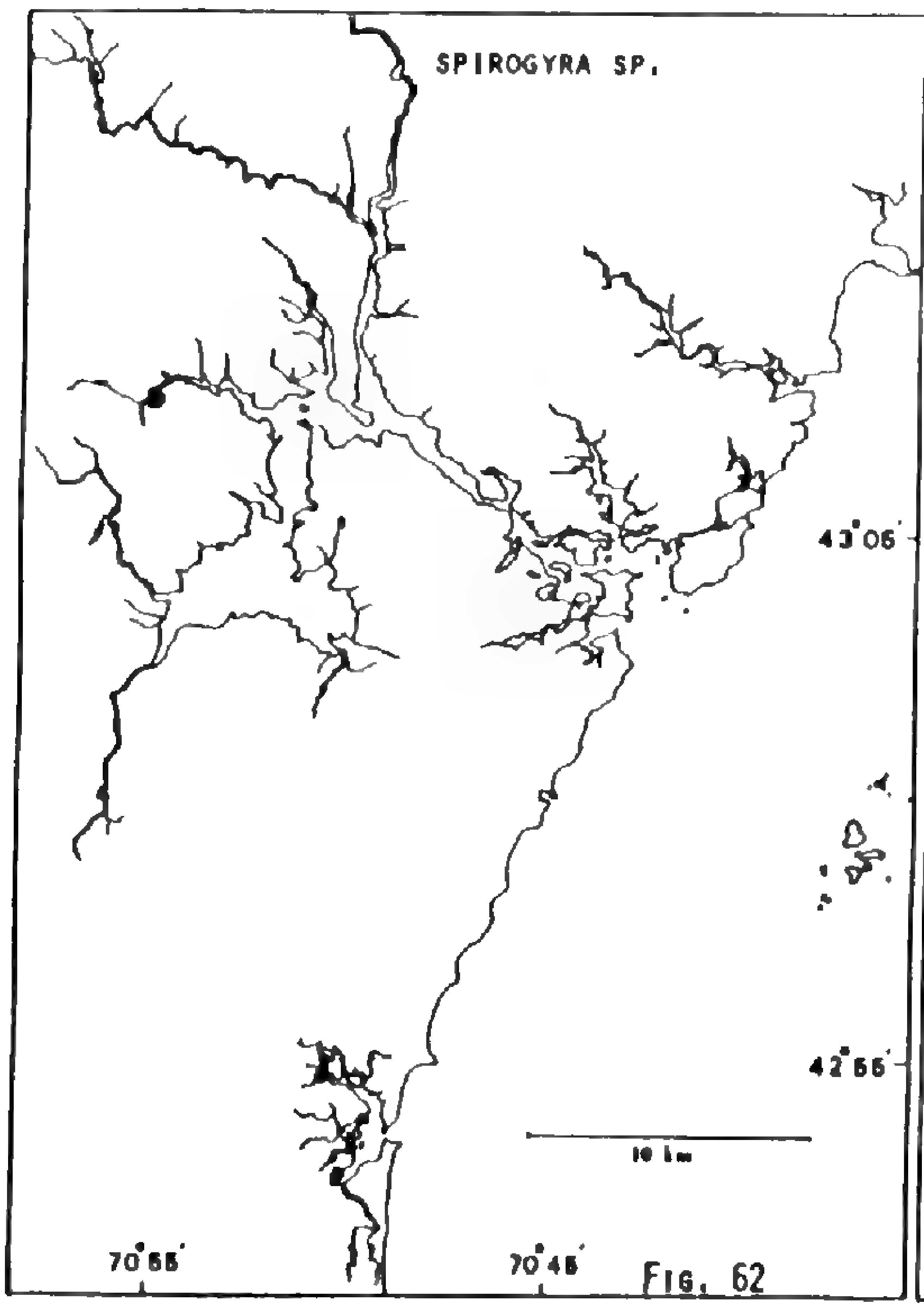


FIG. 62

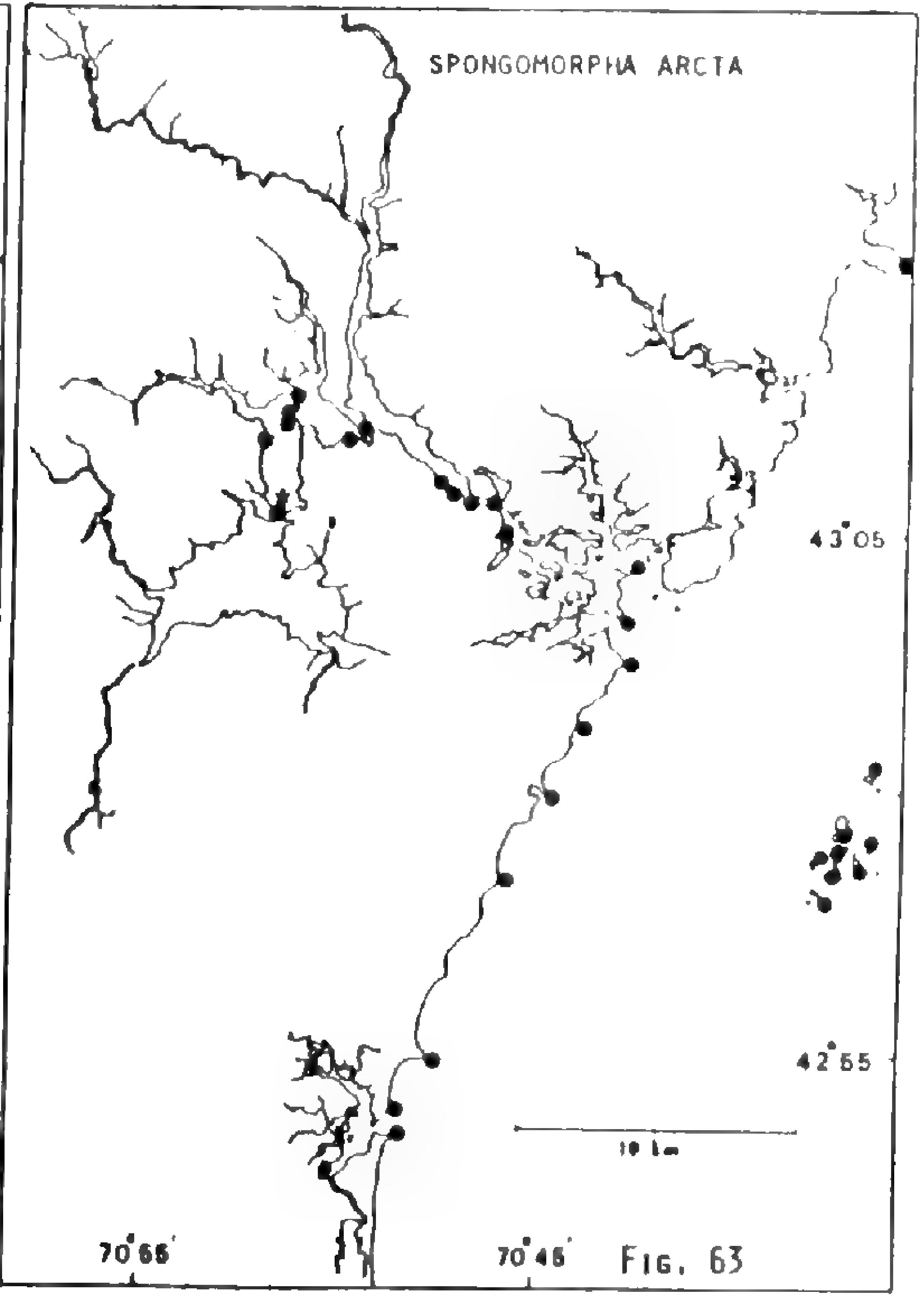


FIG. 63

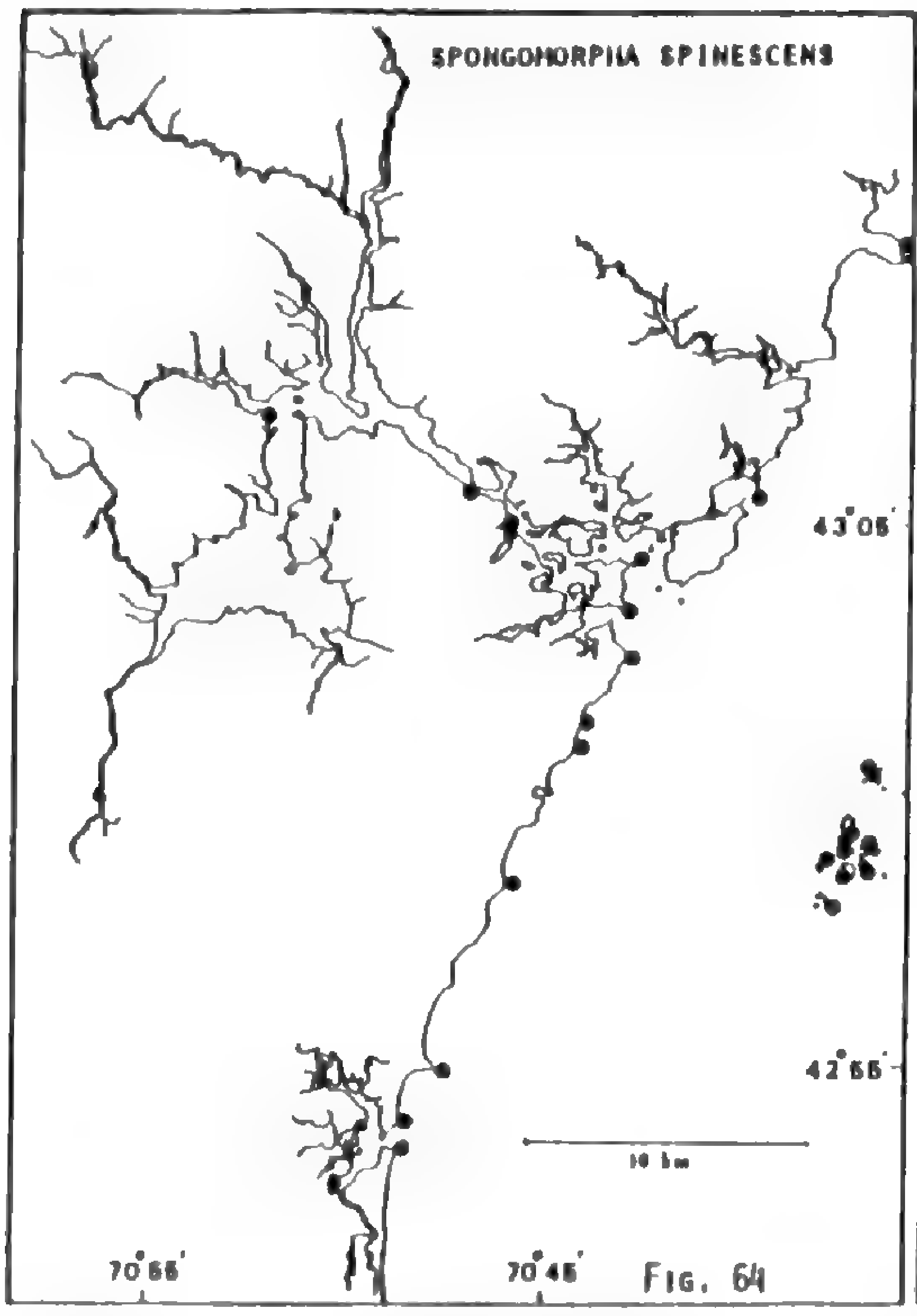


Fig. 64

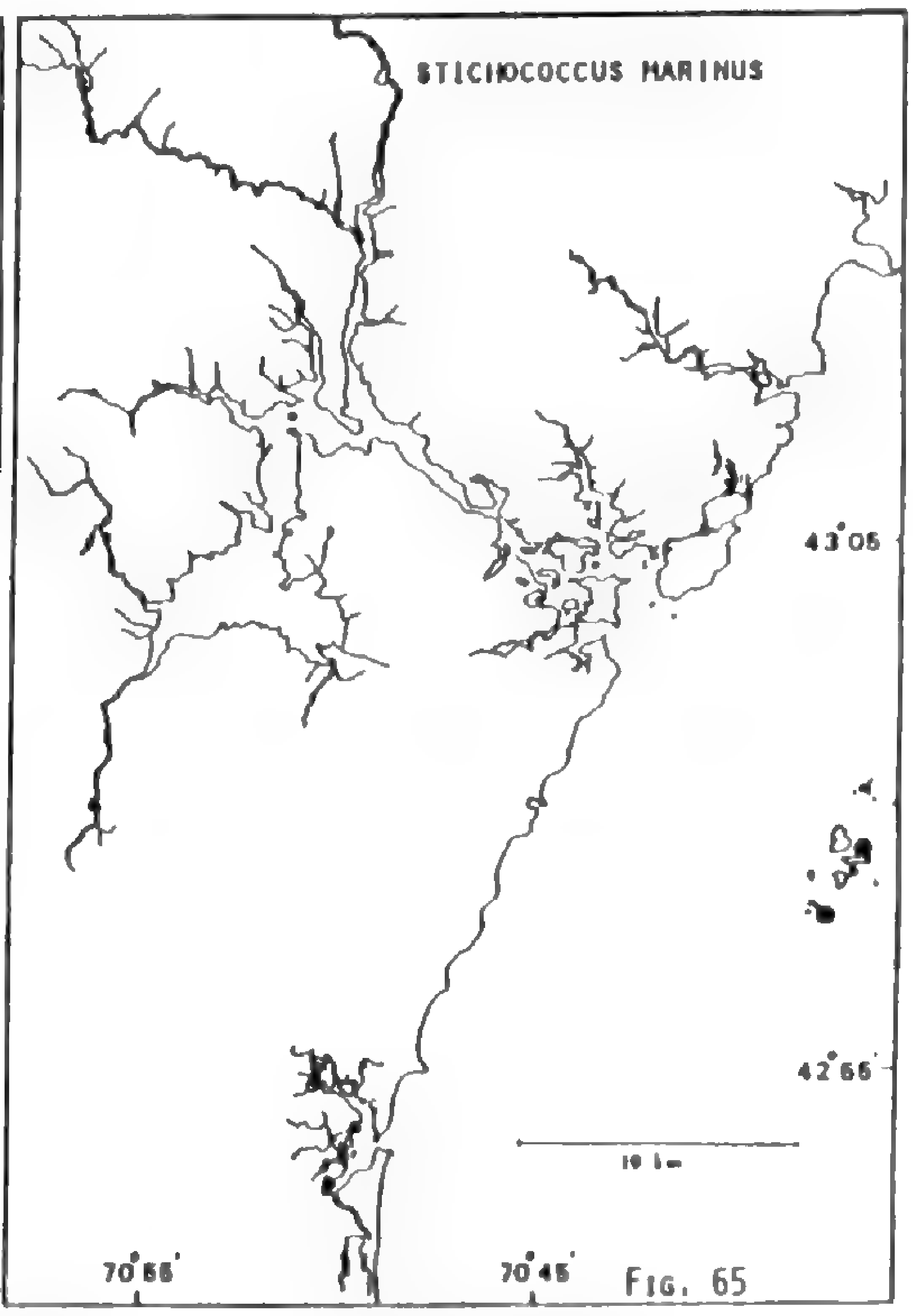


Fig. 65

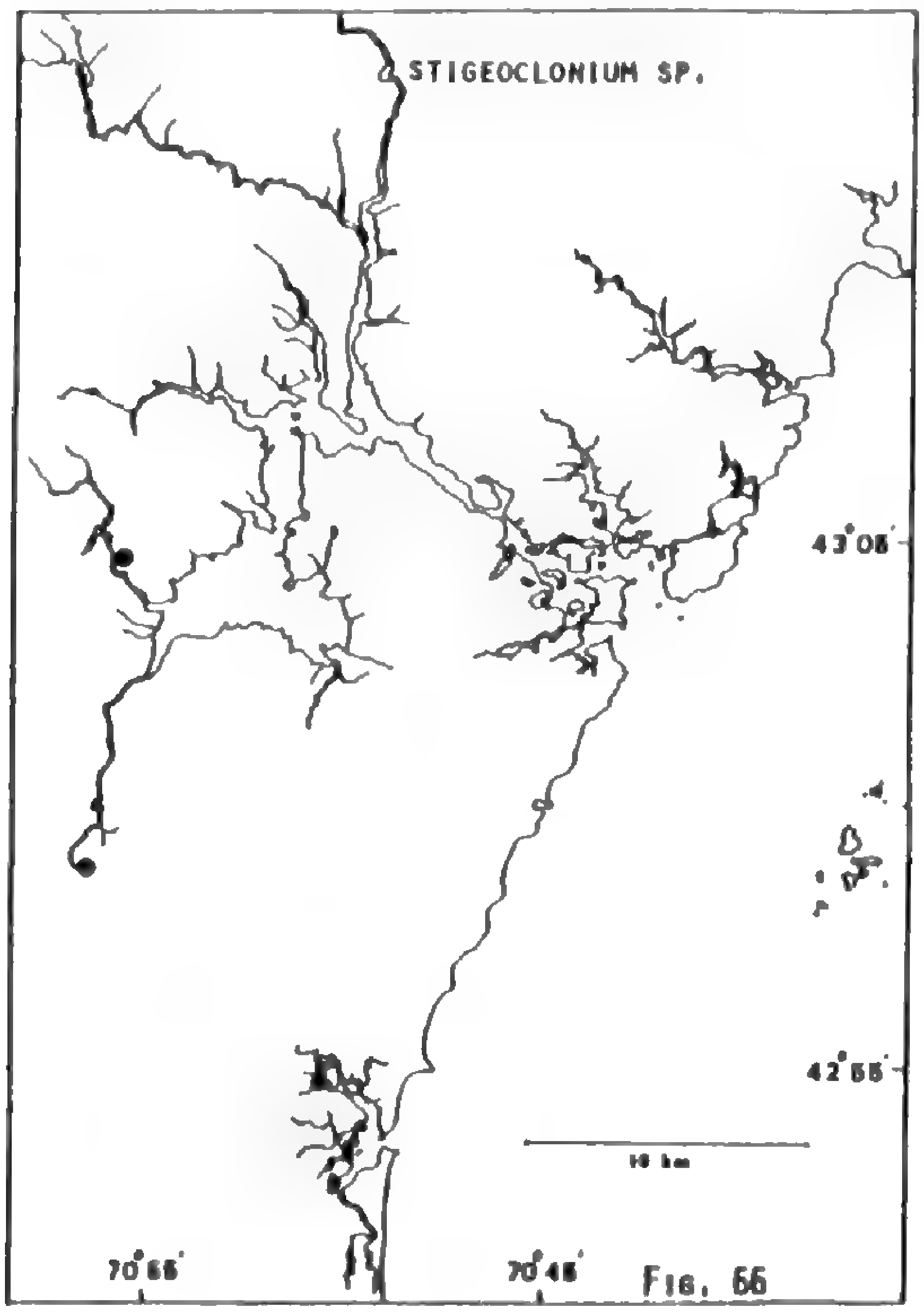


Fig. 66

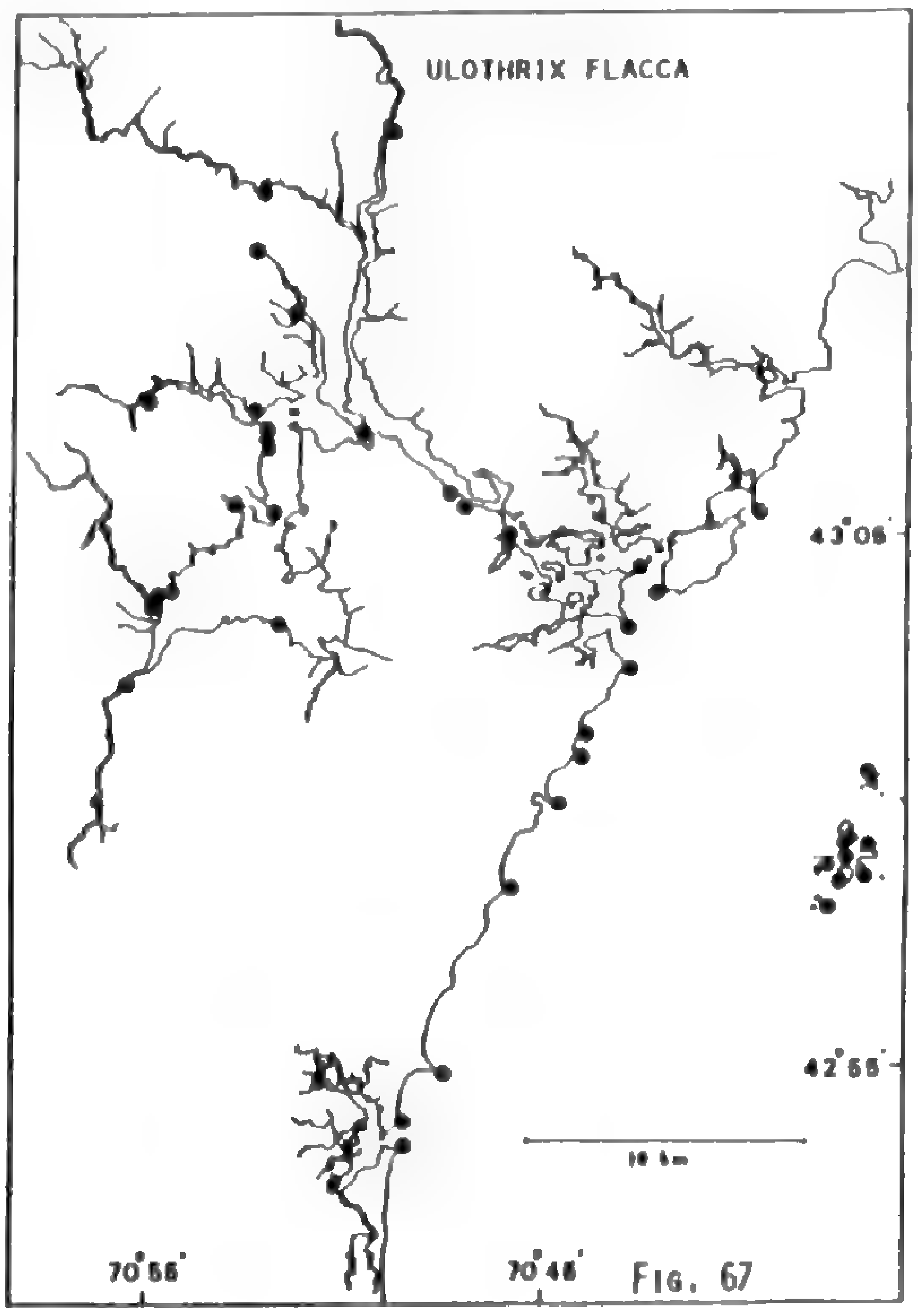


Fig. 67

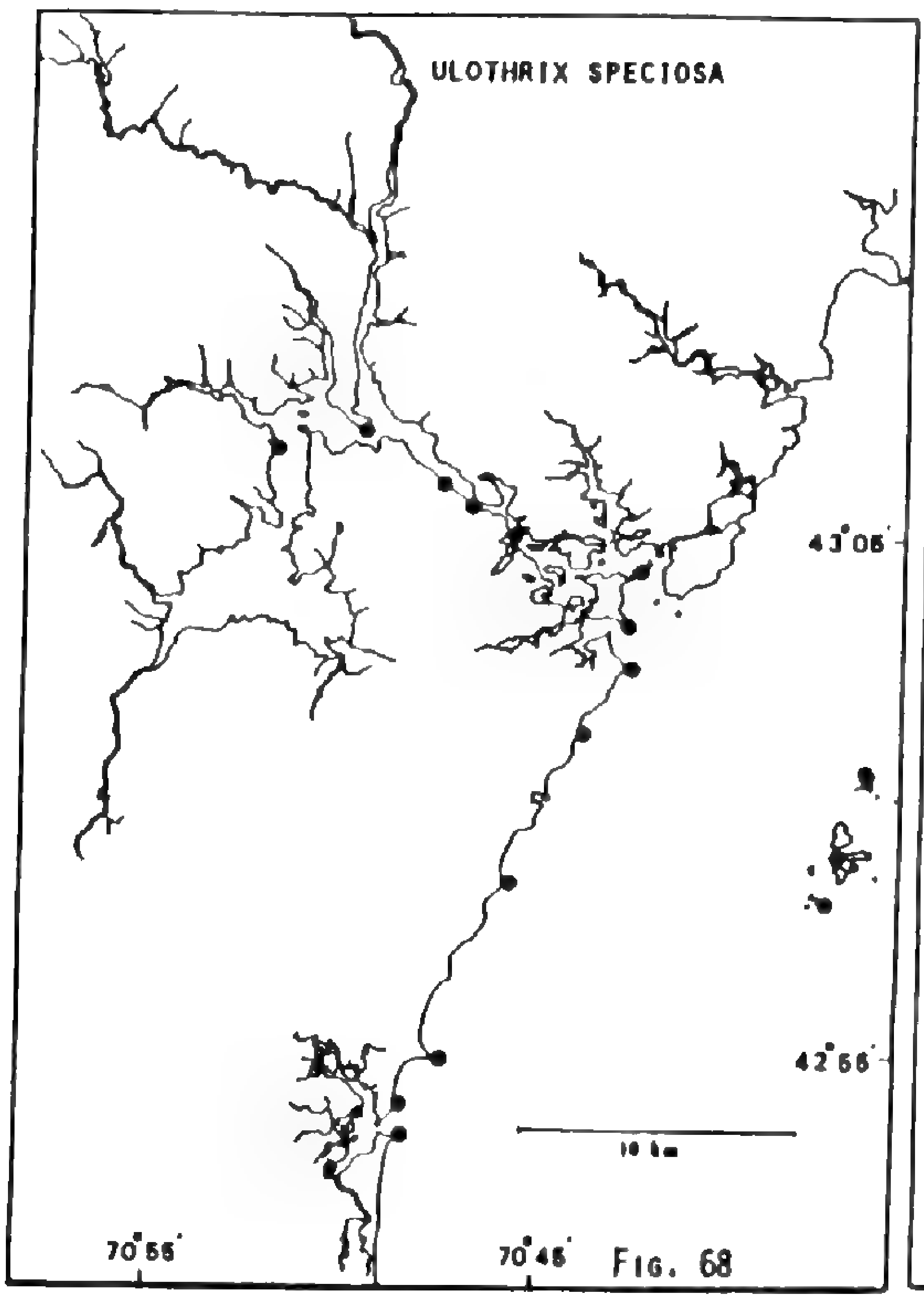


FIG. 68

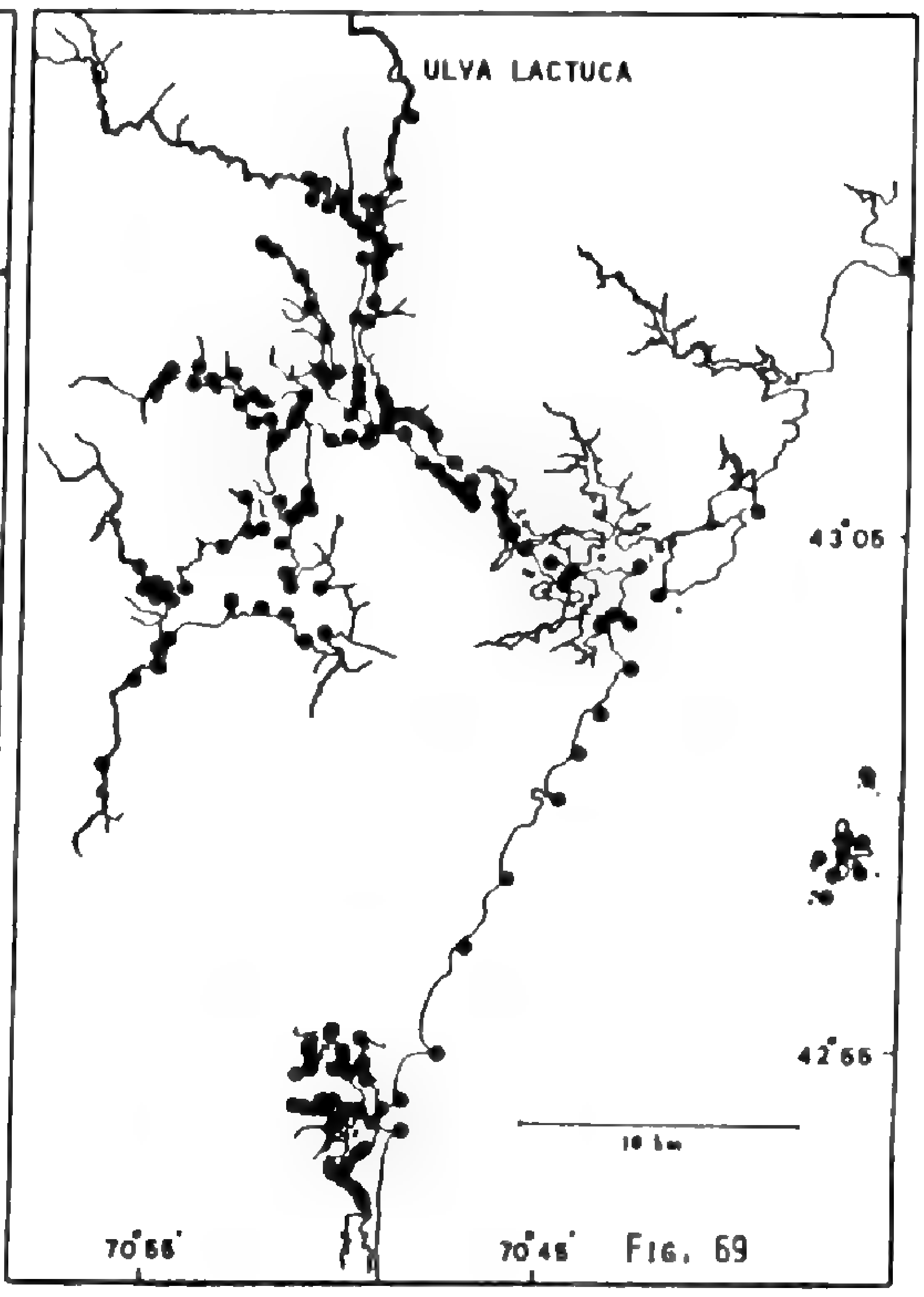


FIG. 69

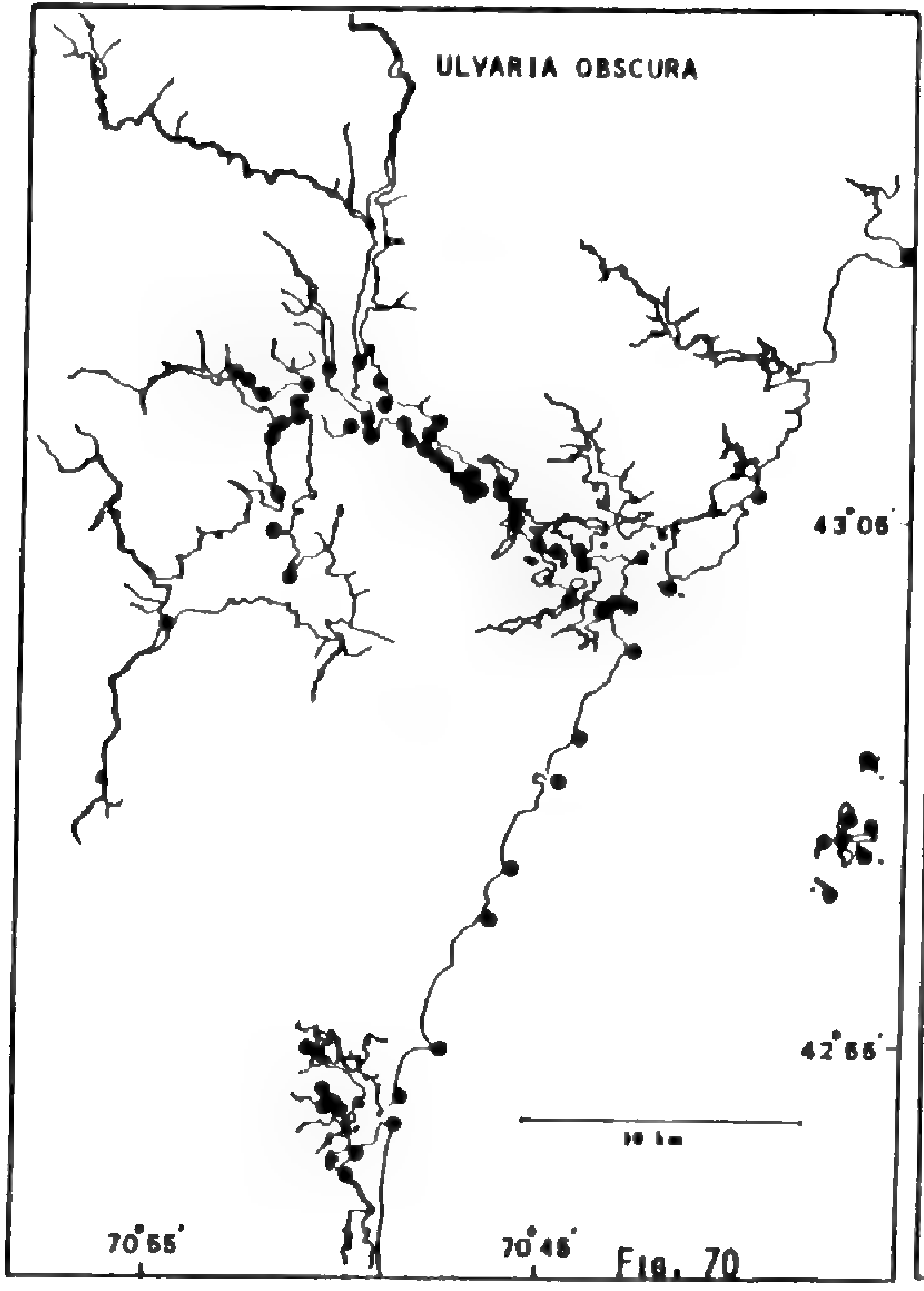


FIG. 70

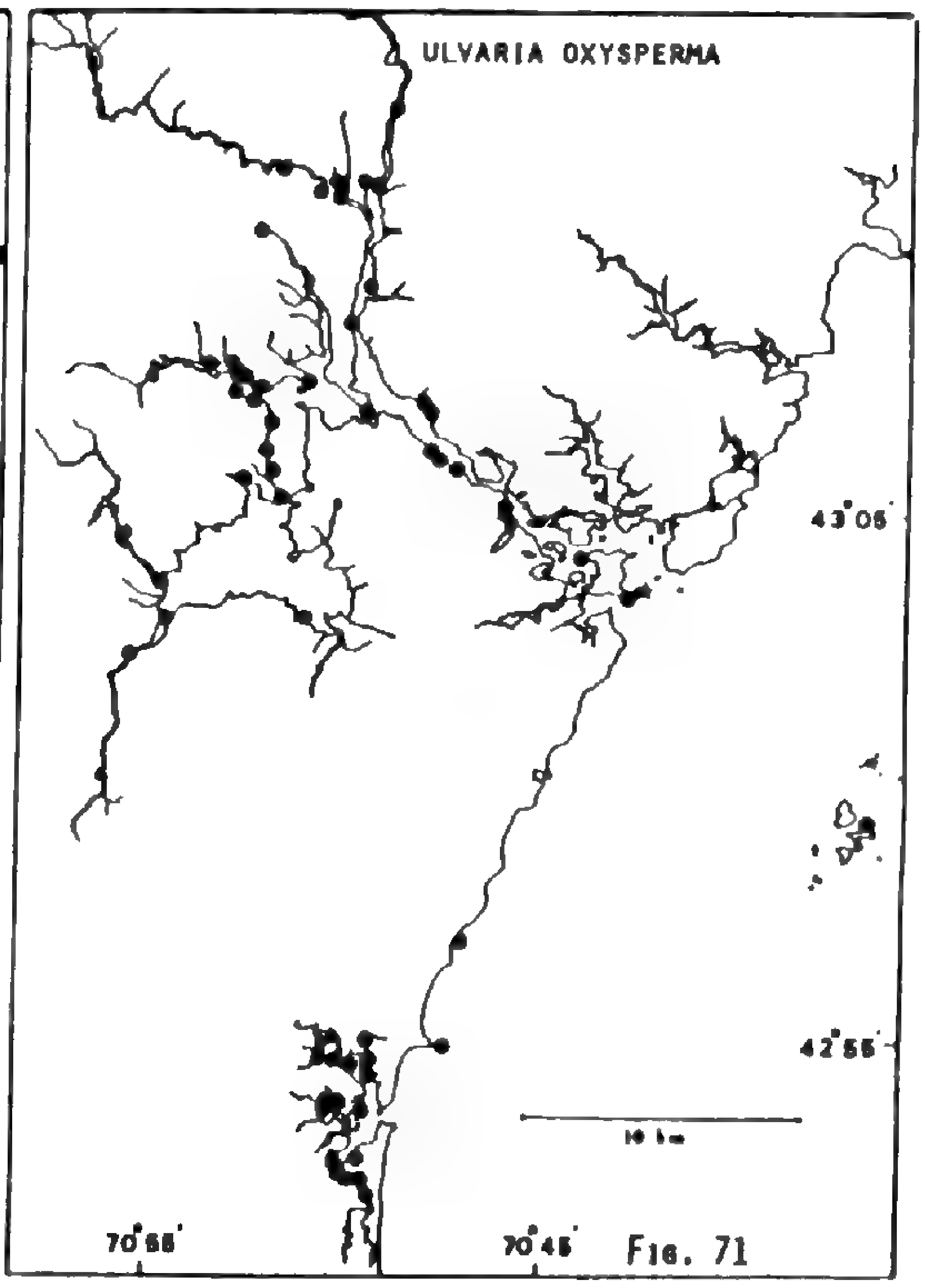


FIG. 71

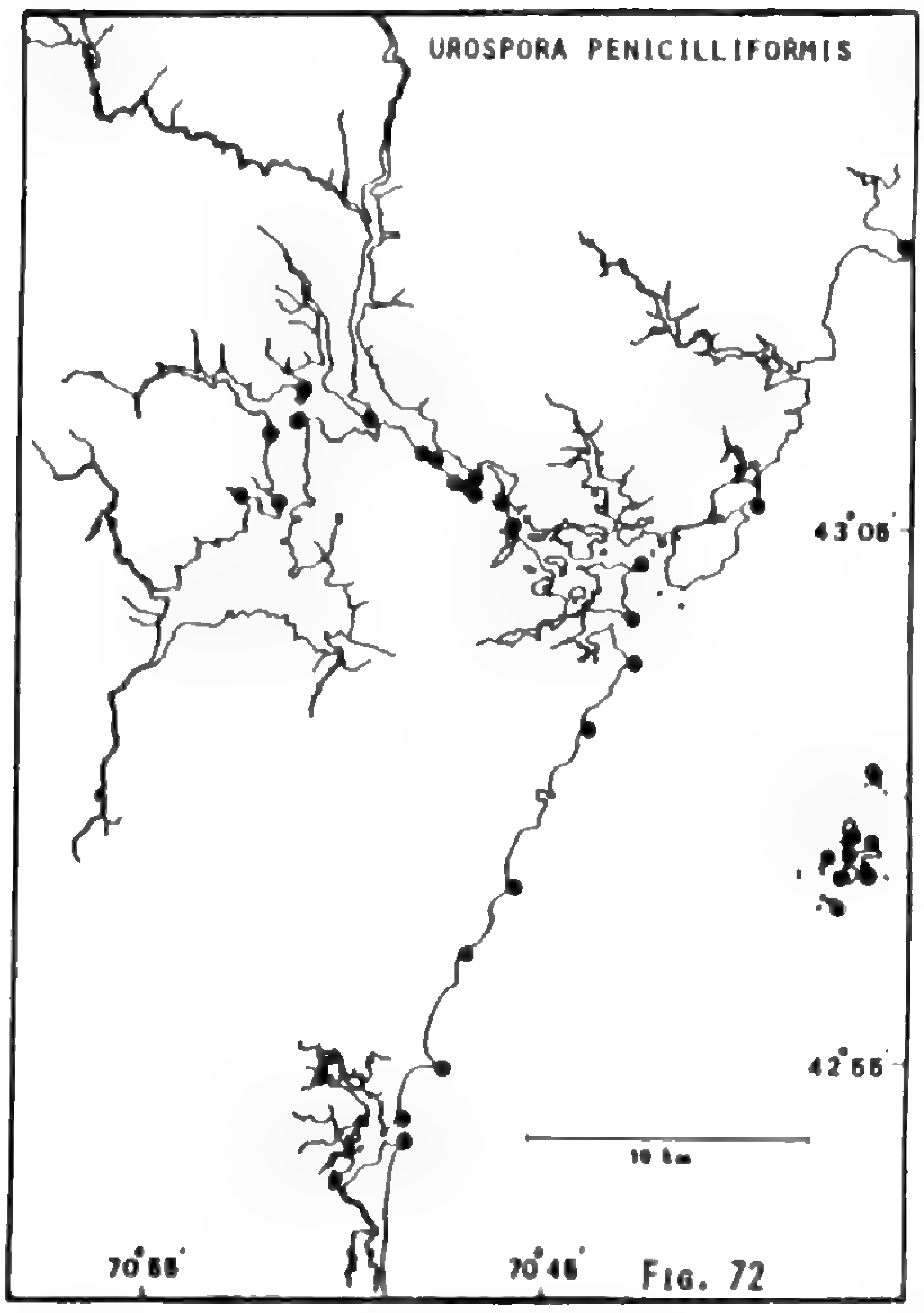


Fig. 72

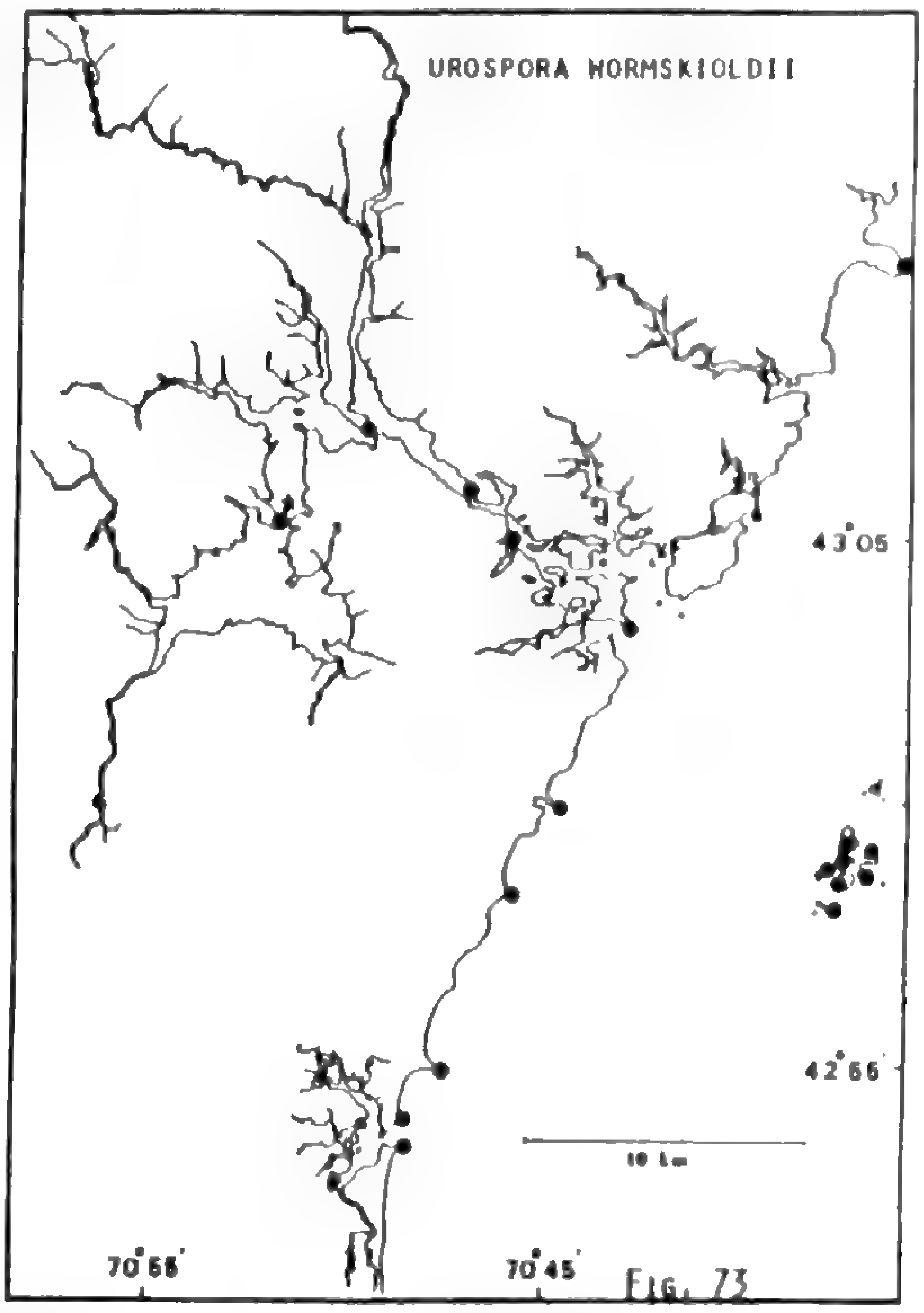


Fig. 73

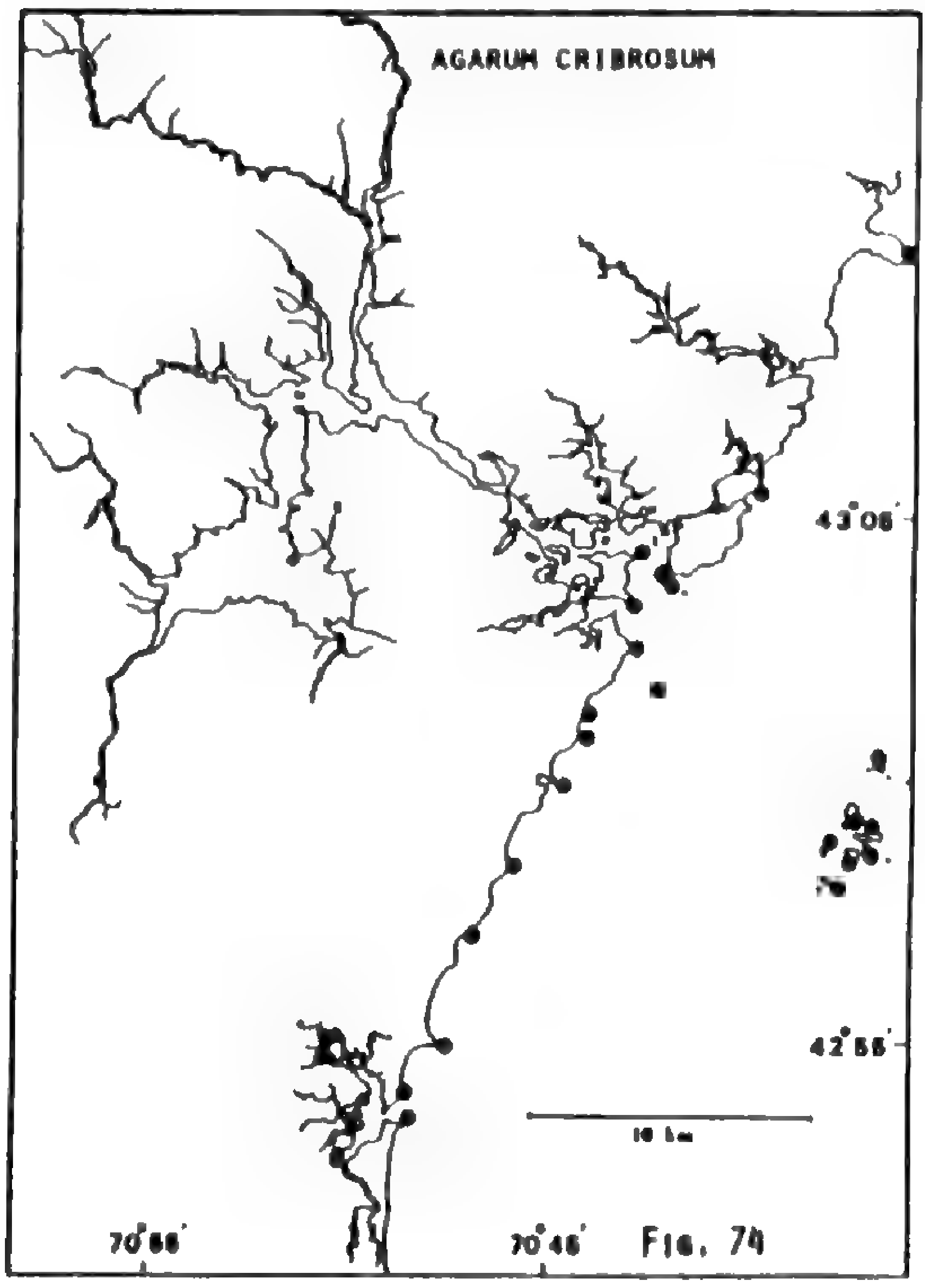


Fig. 74

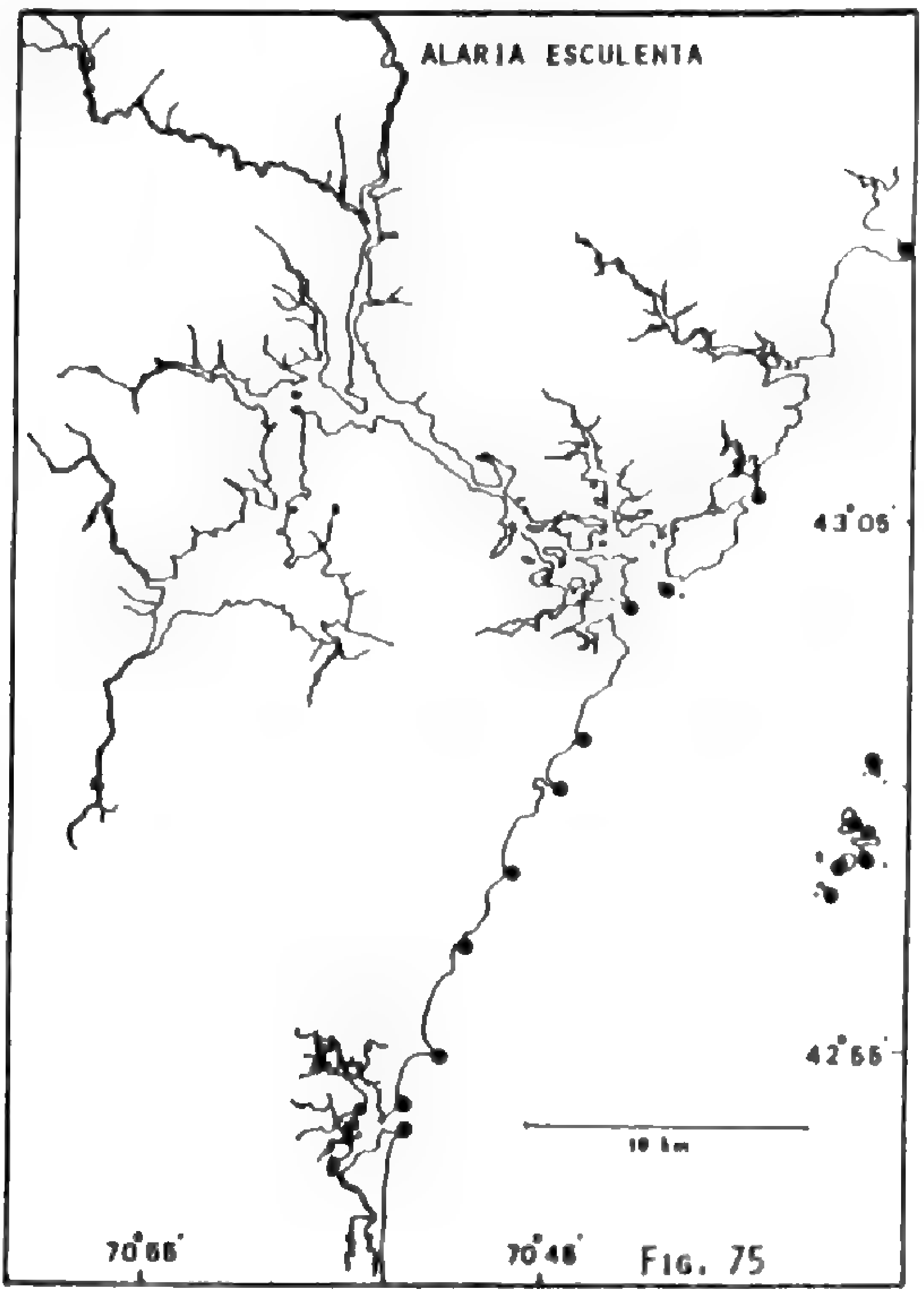


Fig. 75

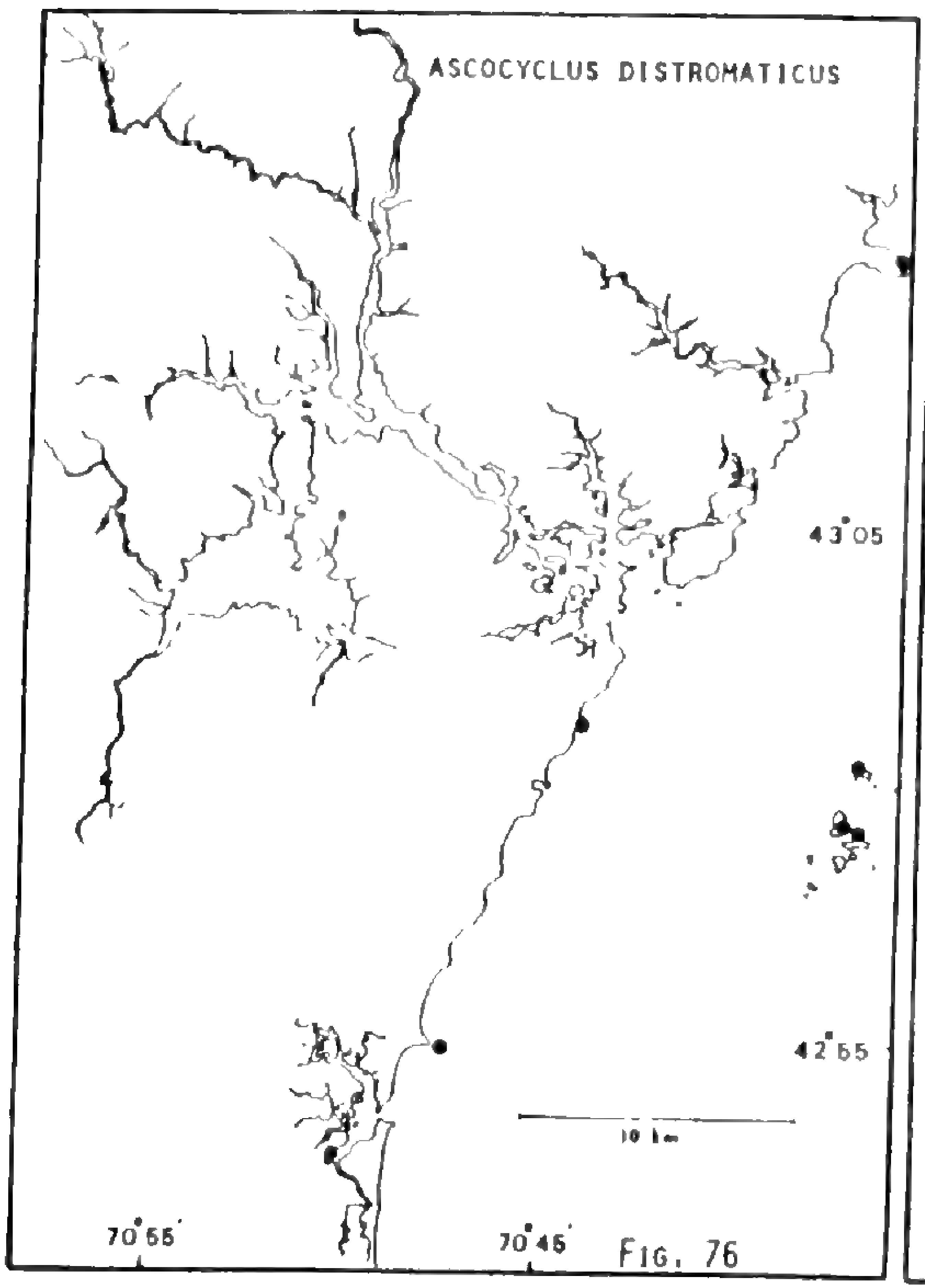


Fig. 76

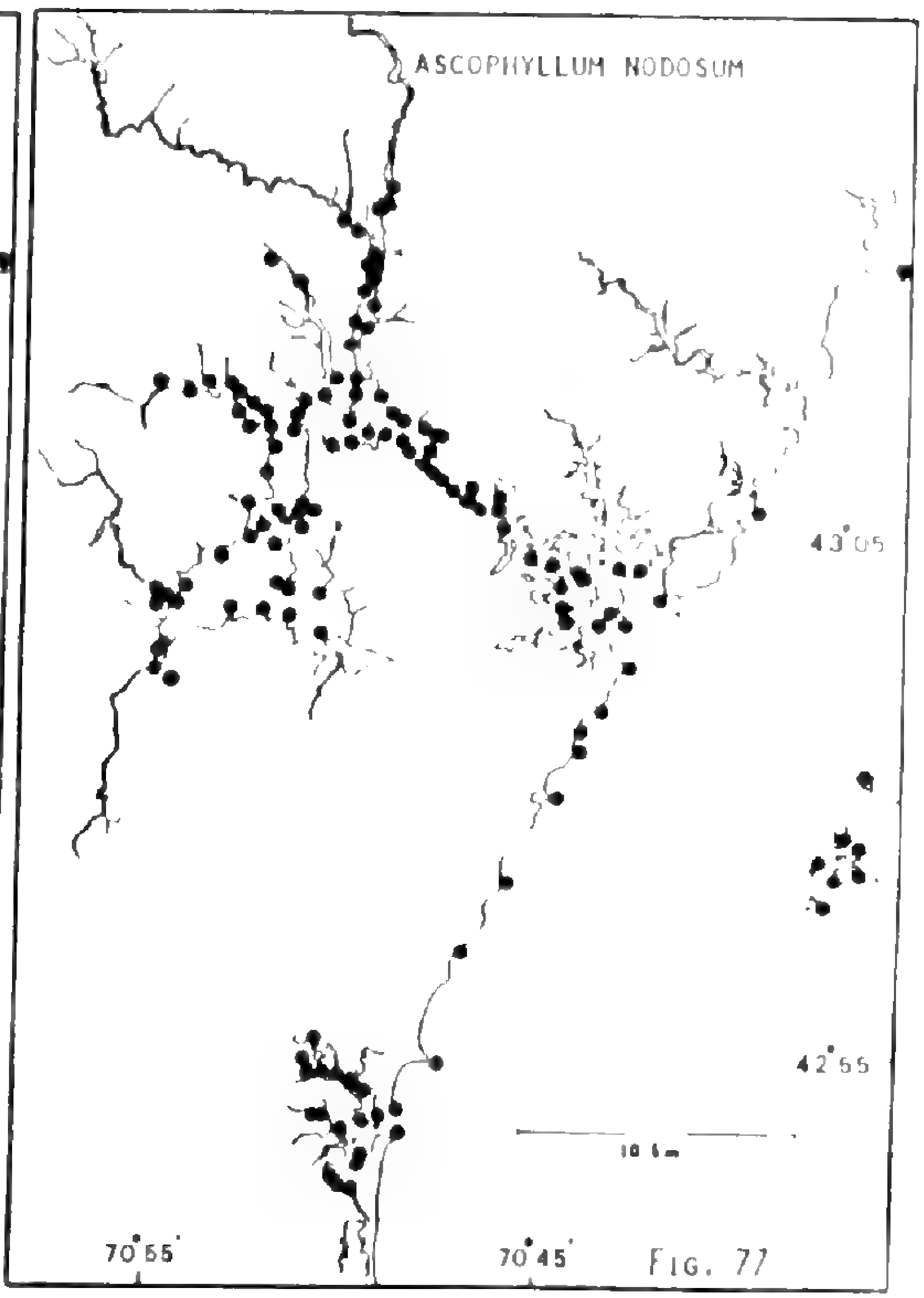


Fig. 77

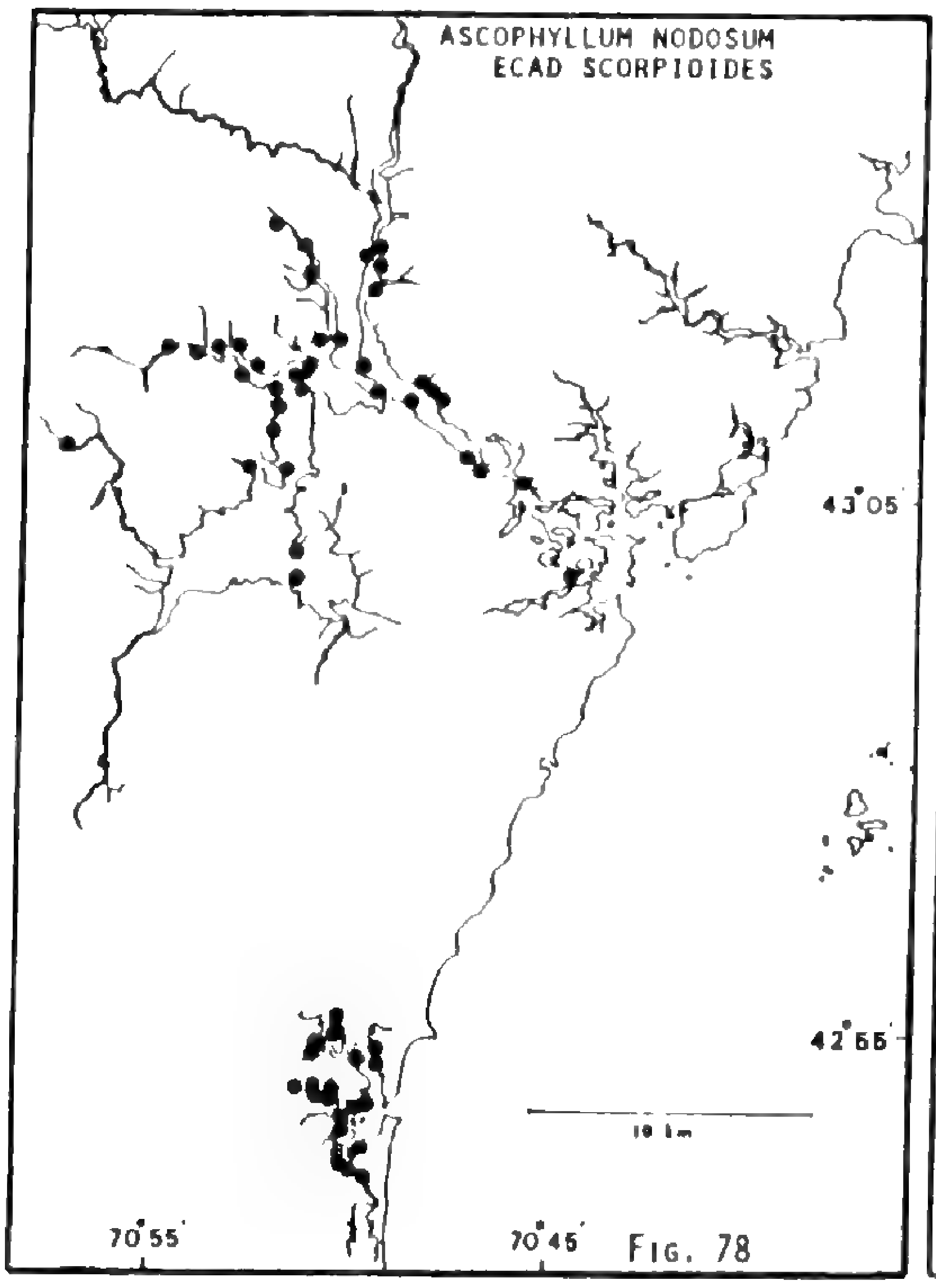


Fig. 78

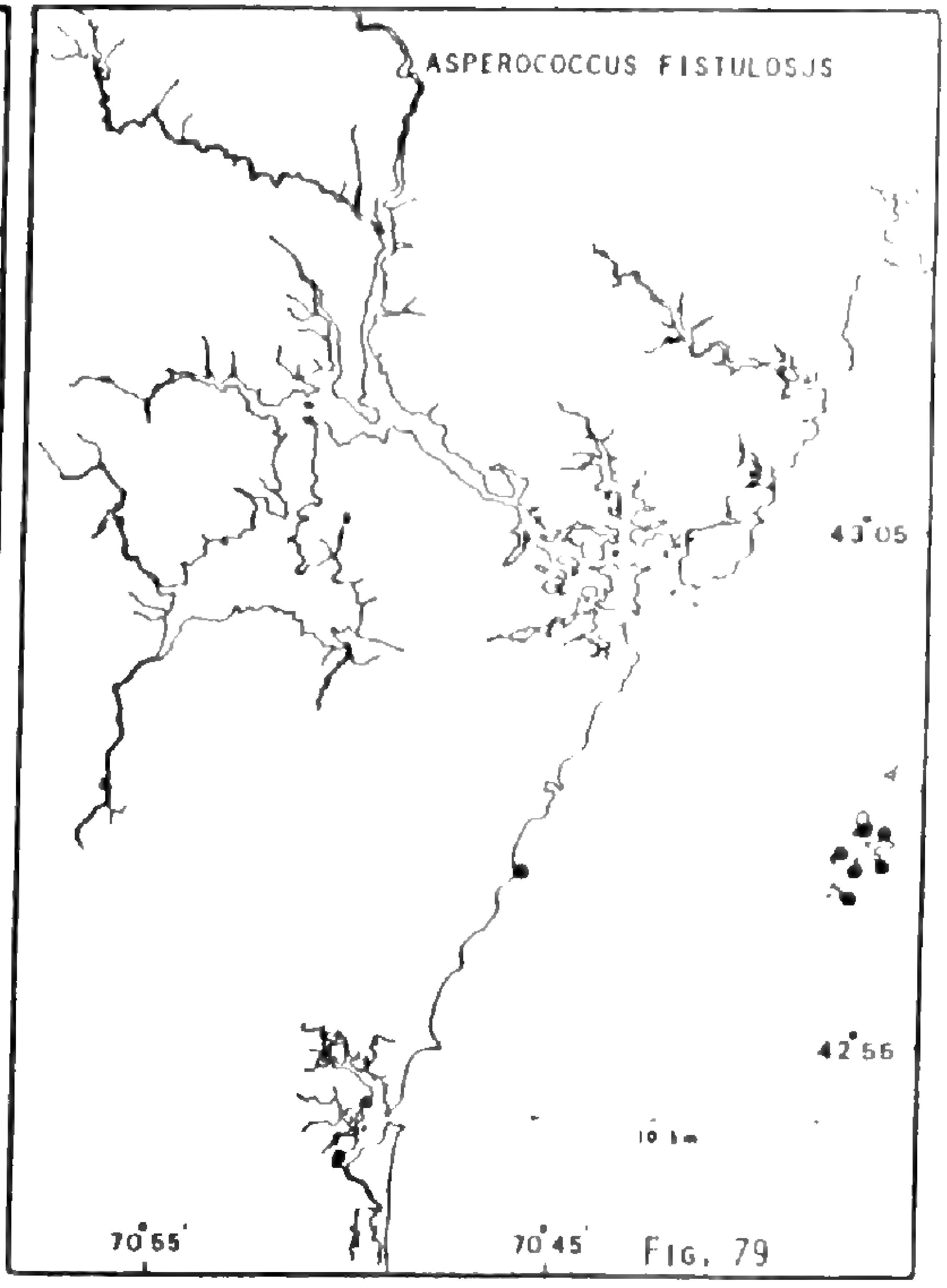


Fig. 79

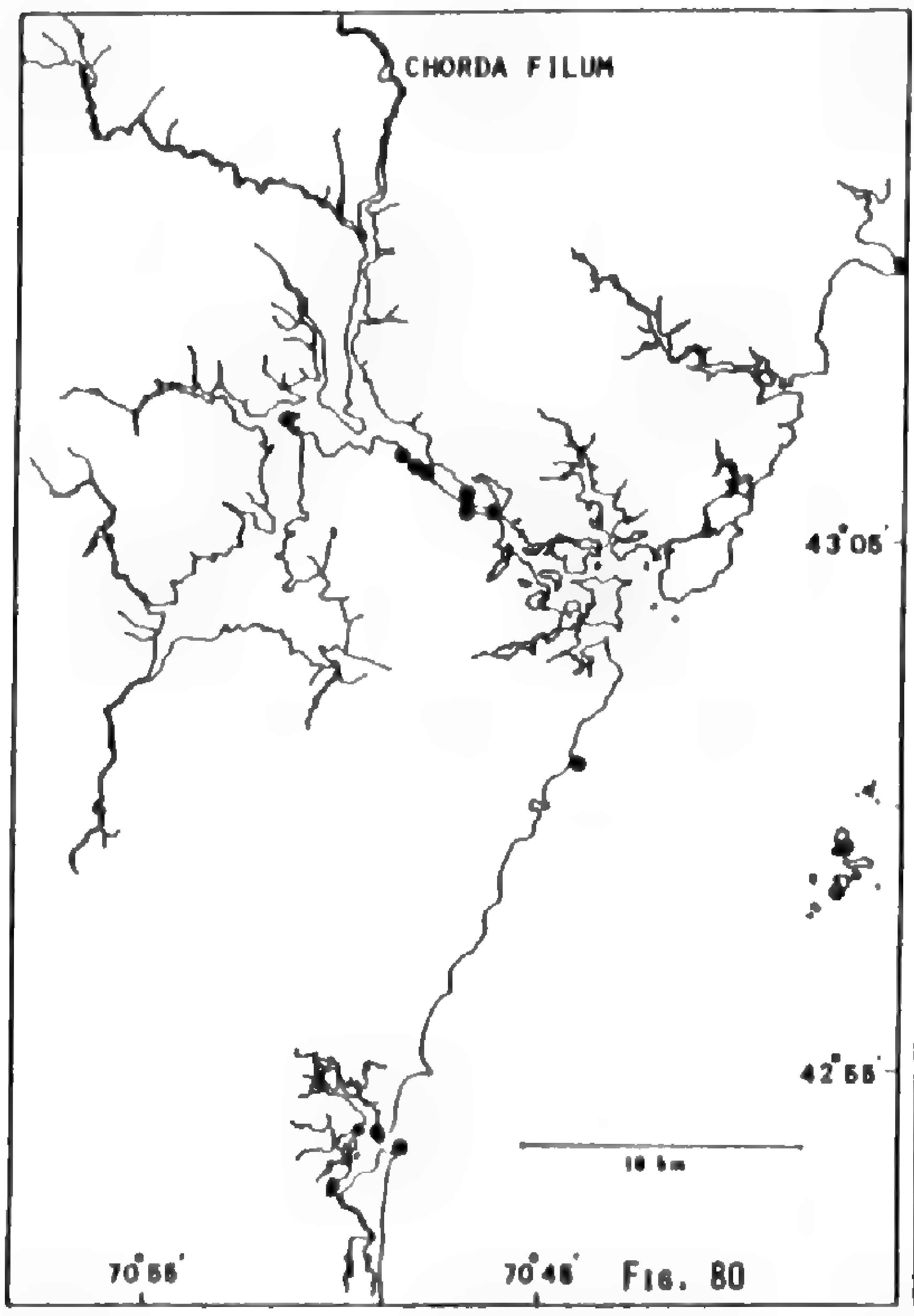


FIG. 80

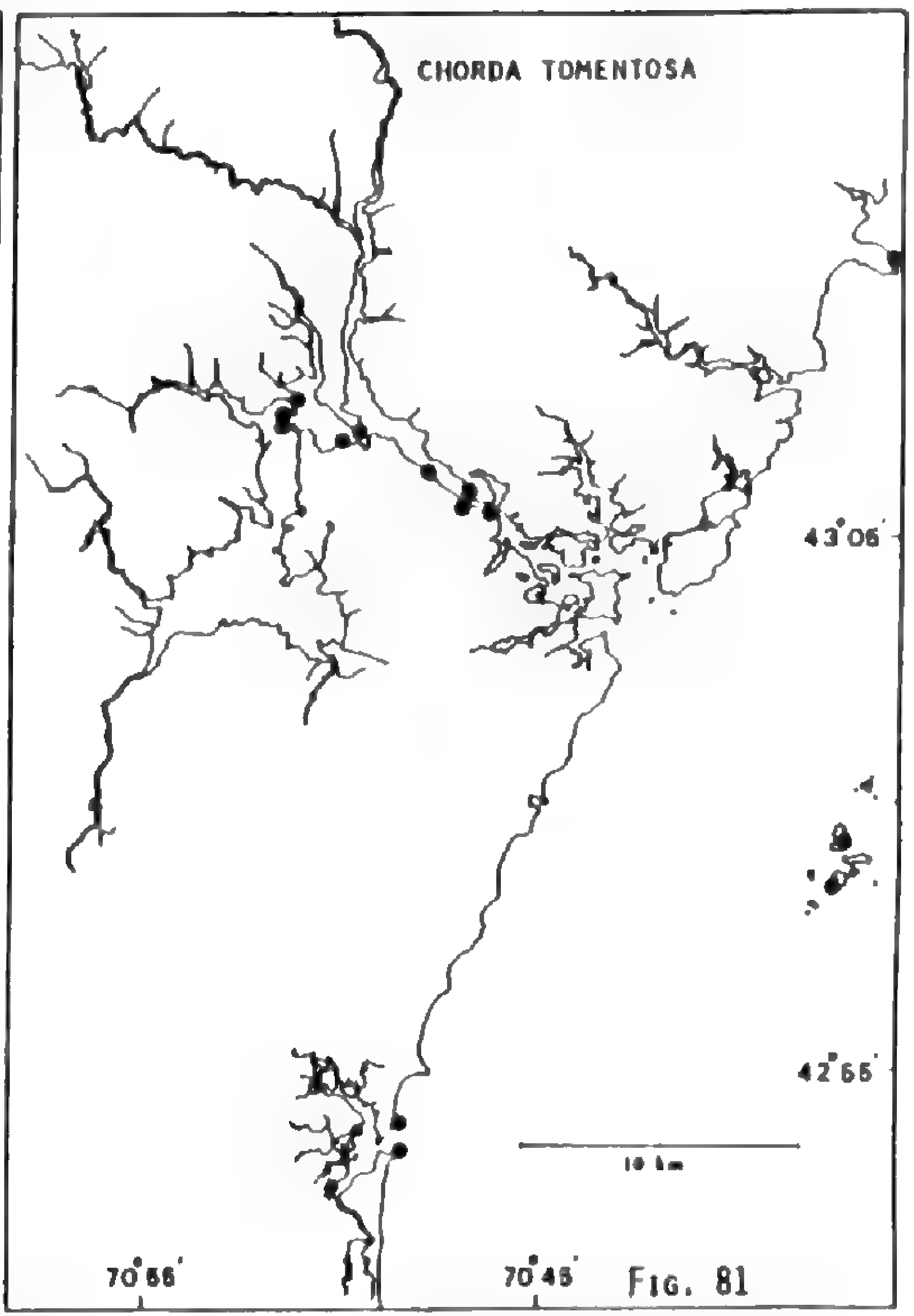


FIG. 81

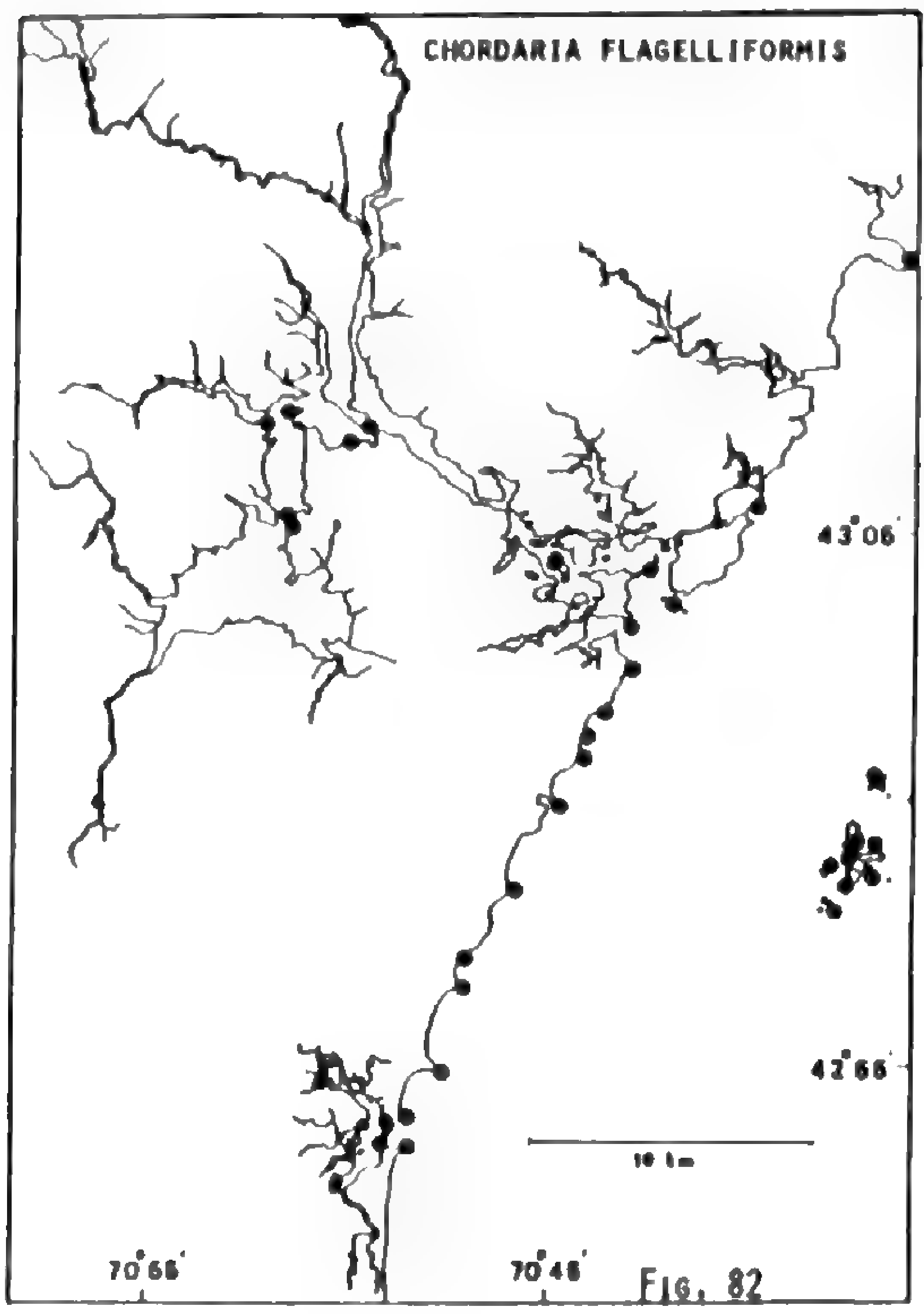


FIG. 82

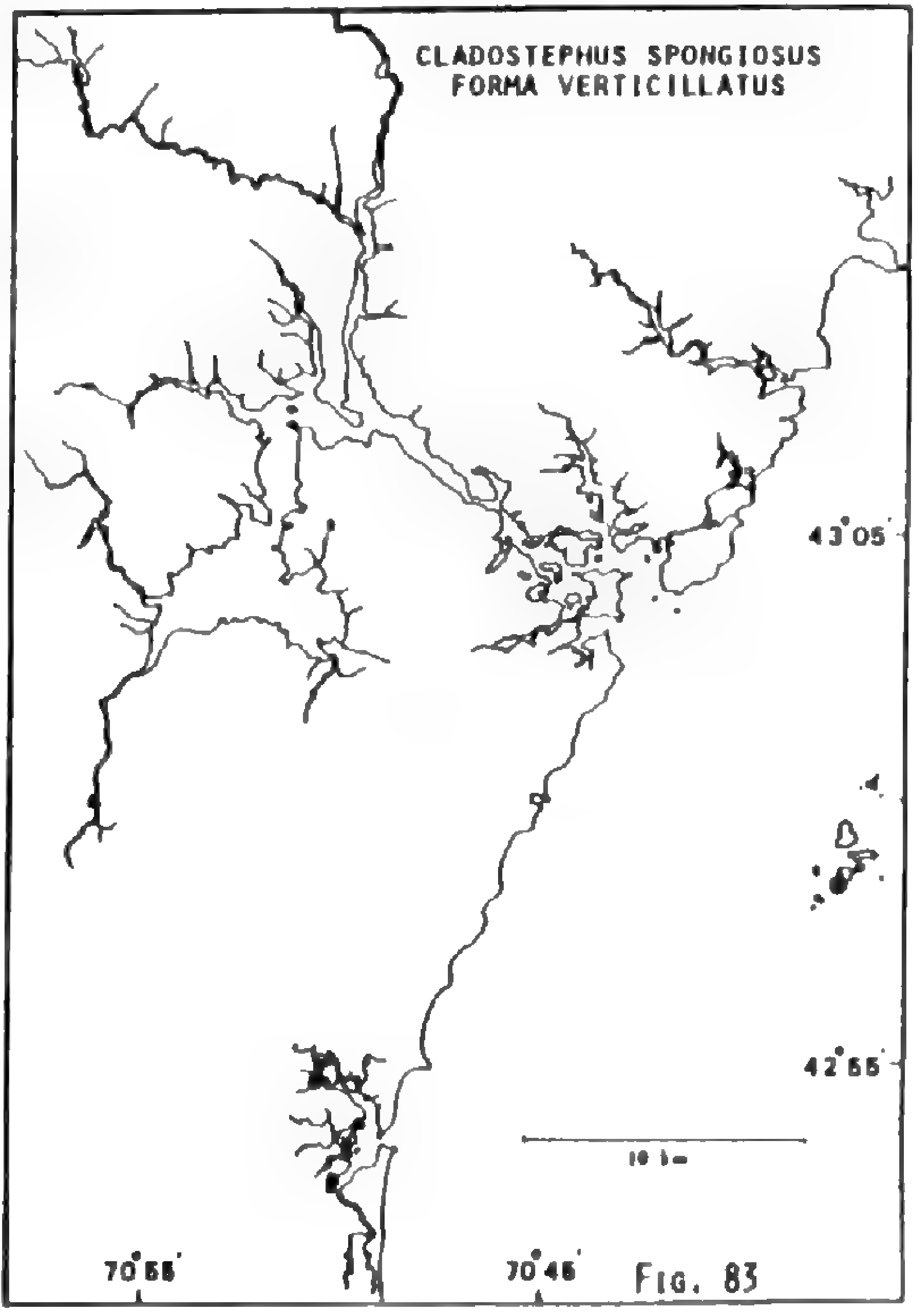


FIG. 83

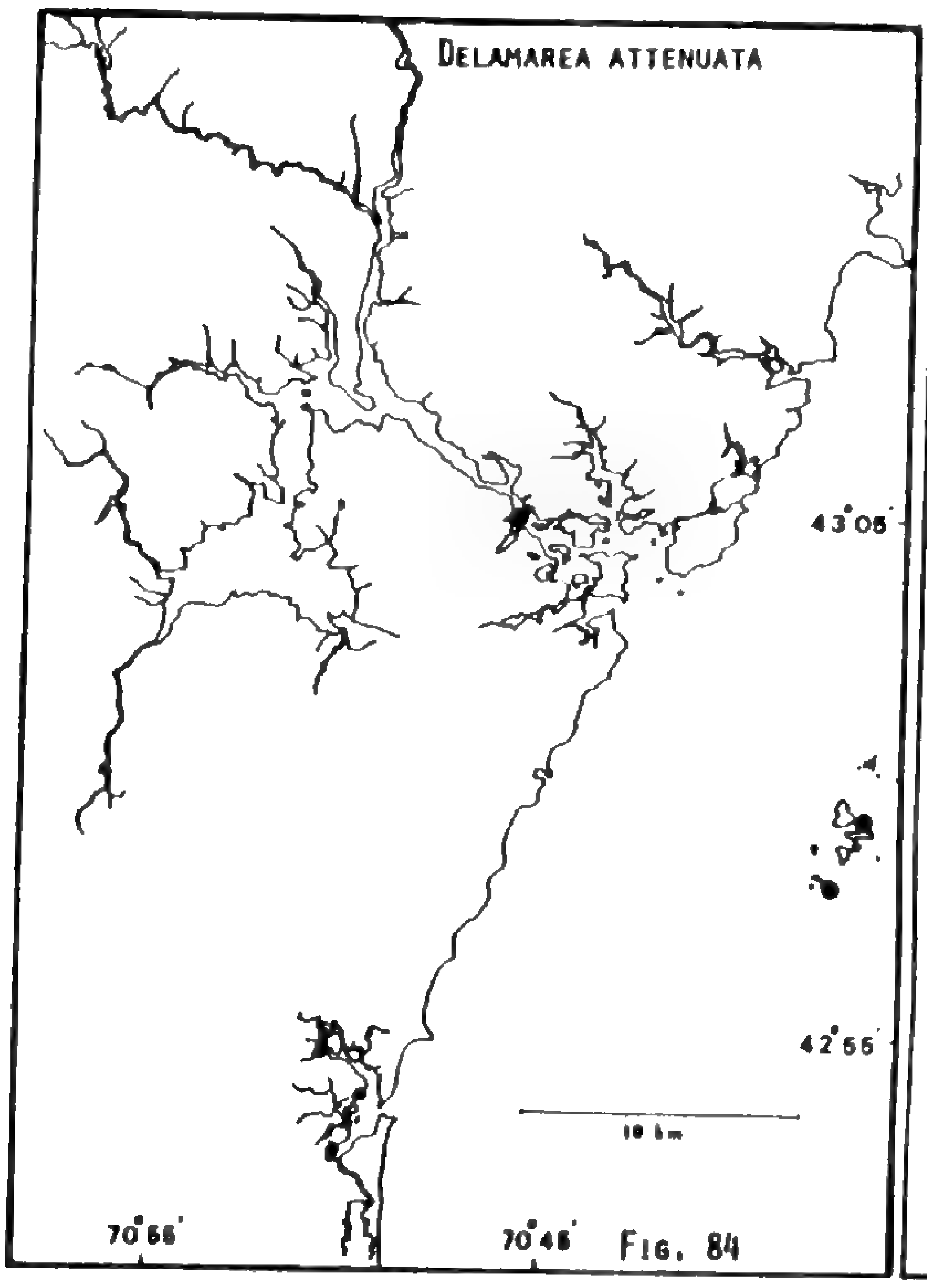


FIG. 84

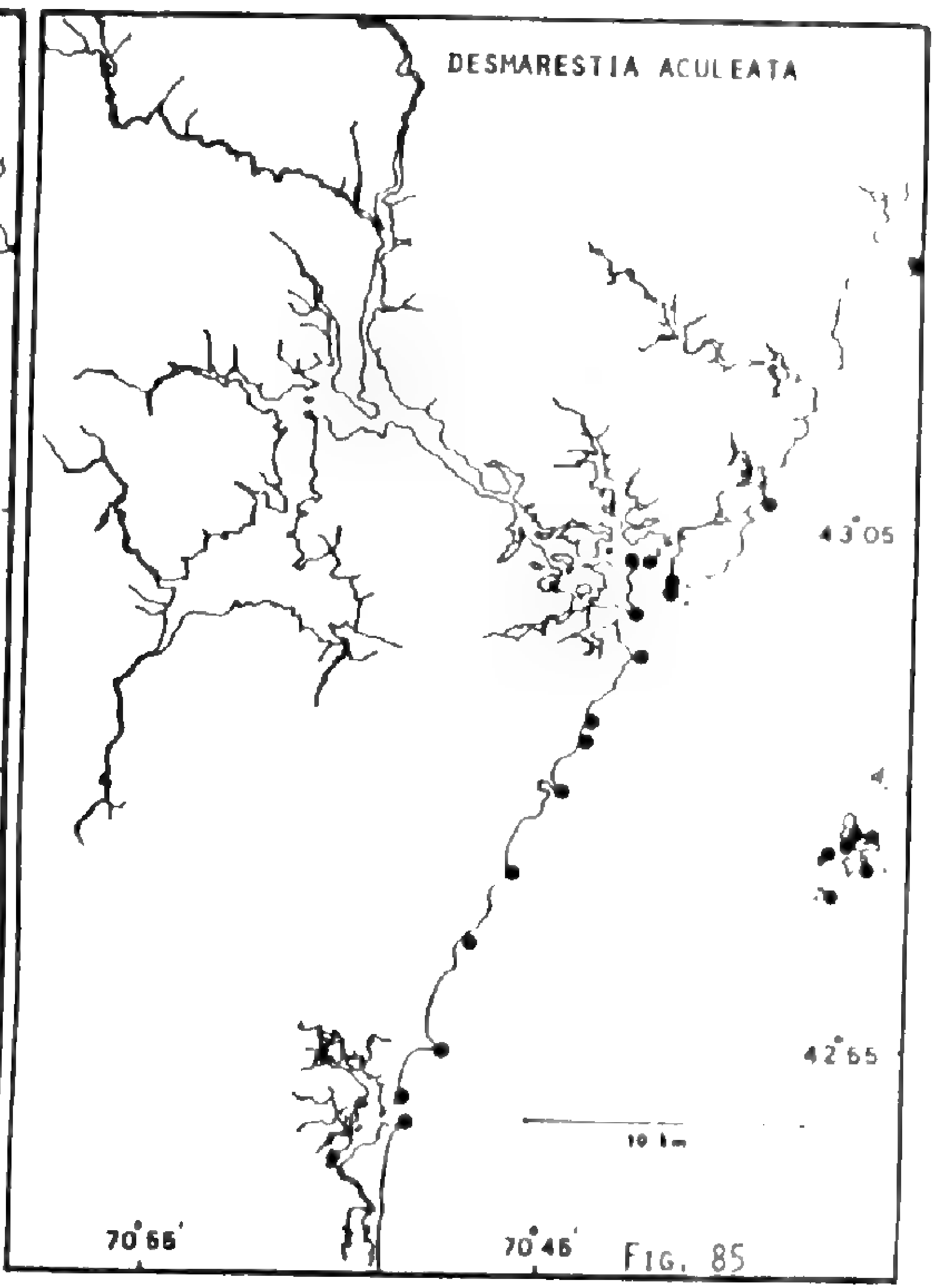


FIG. 85

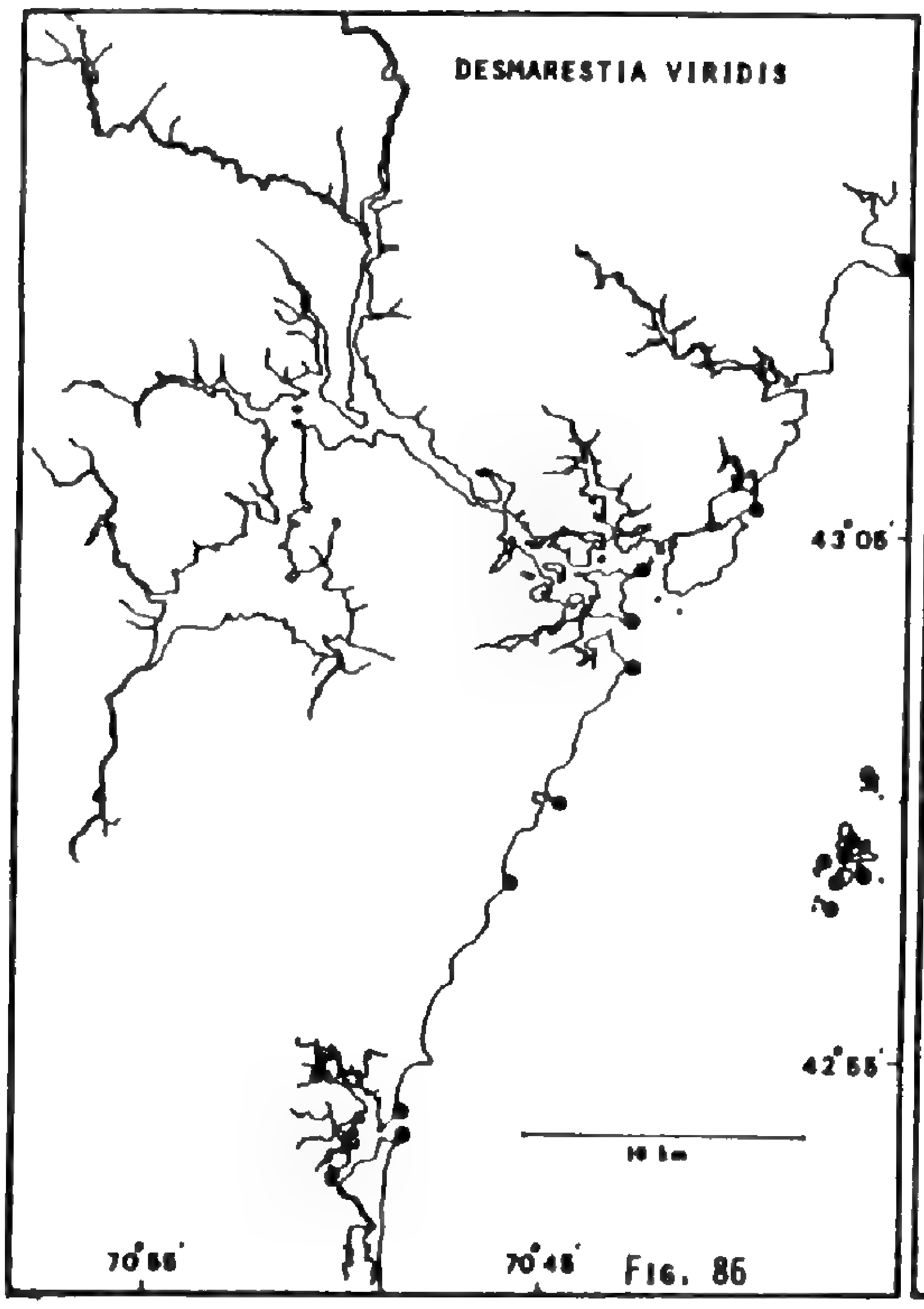


FIG. 86

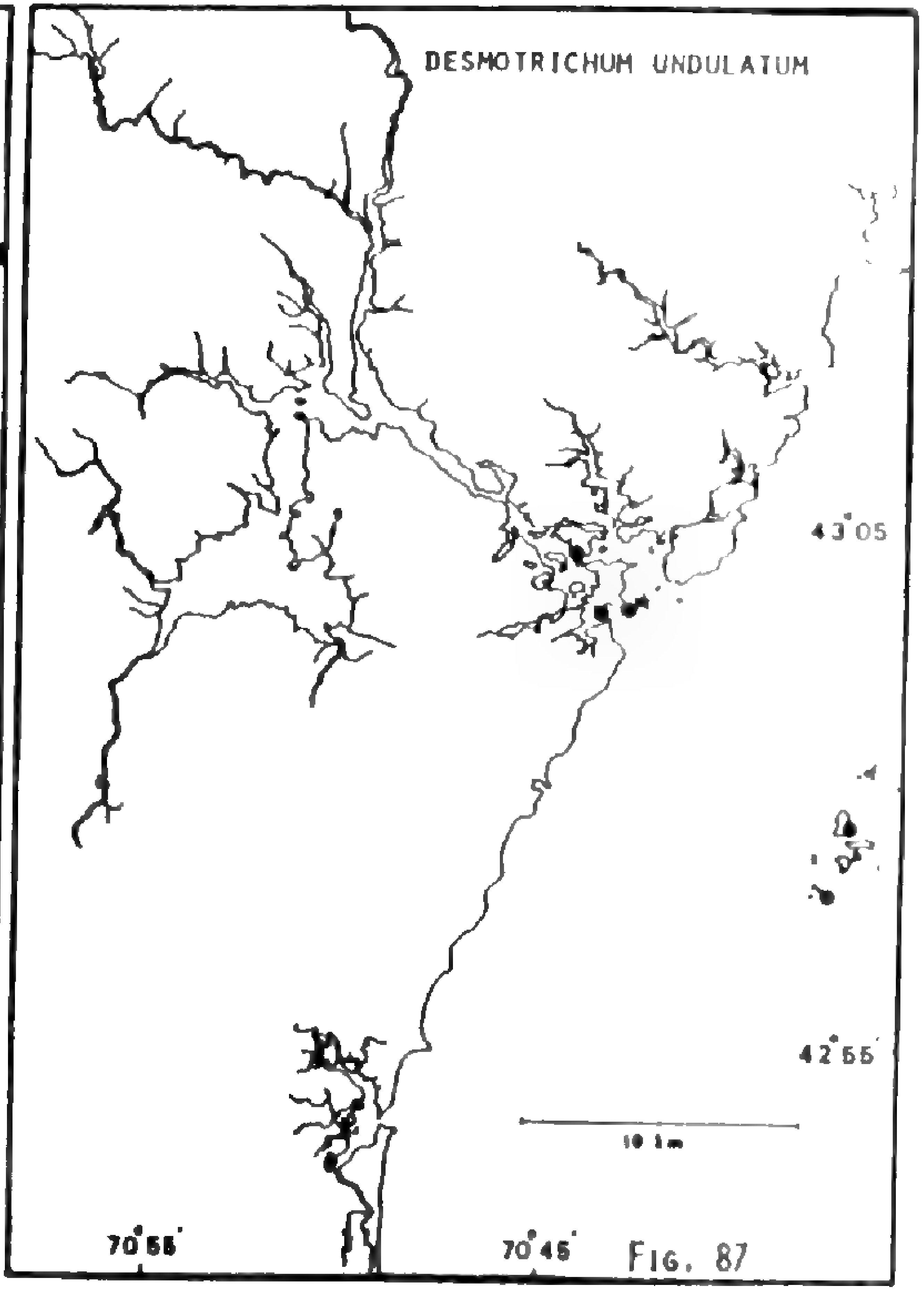


FIG. 87

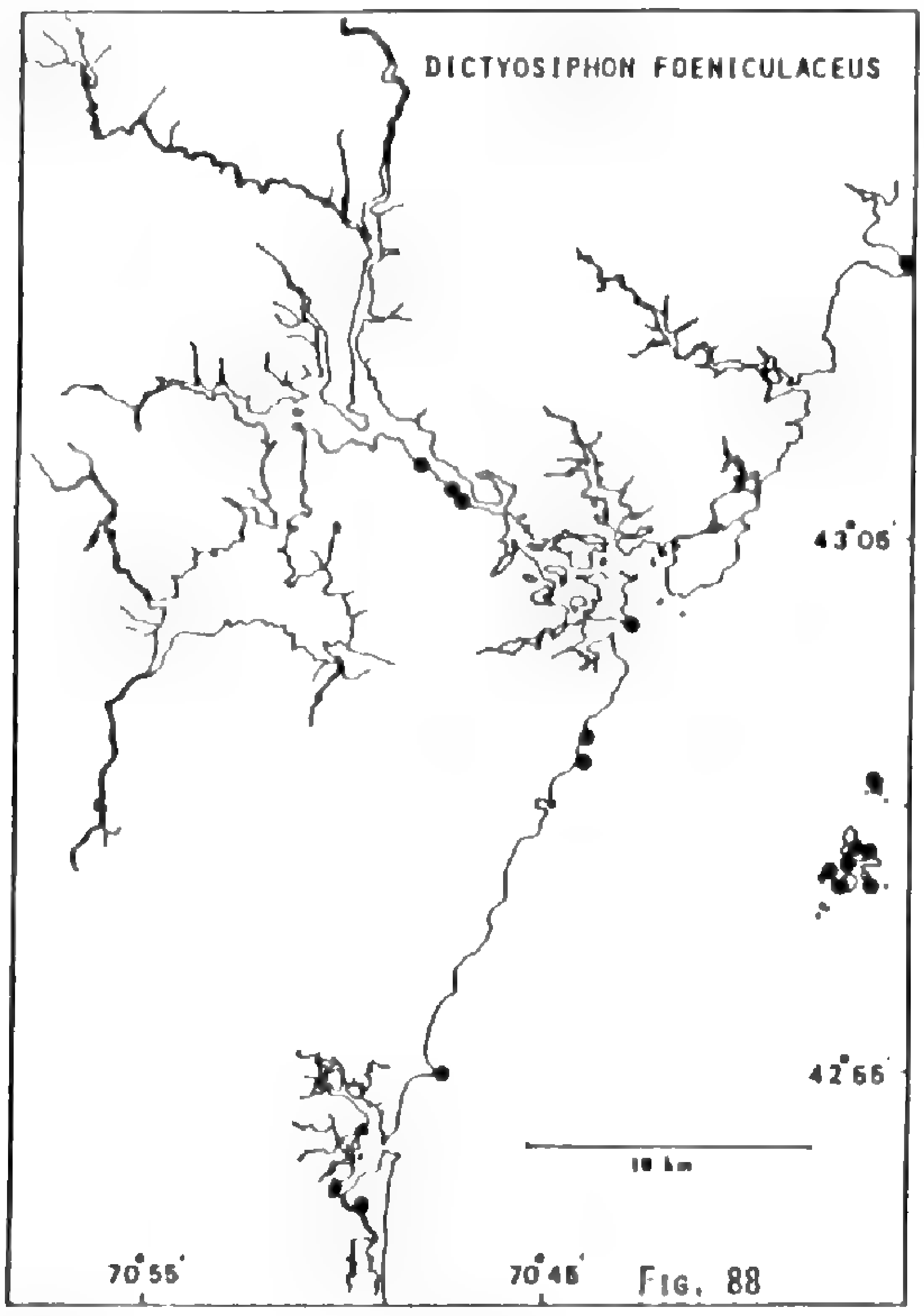

DICTYOSIPHON FOENICULACEUS

FIG. 88

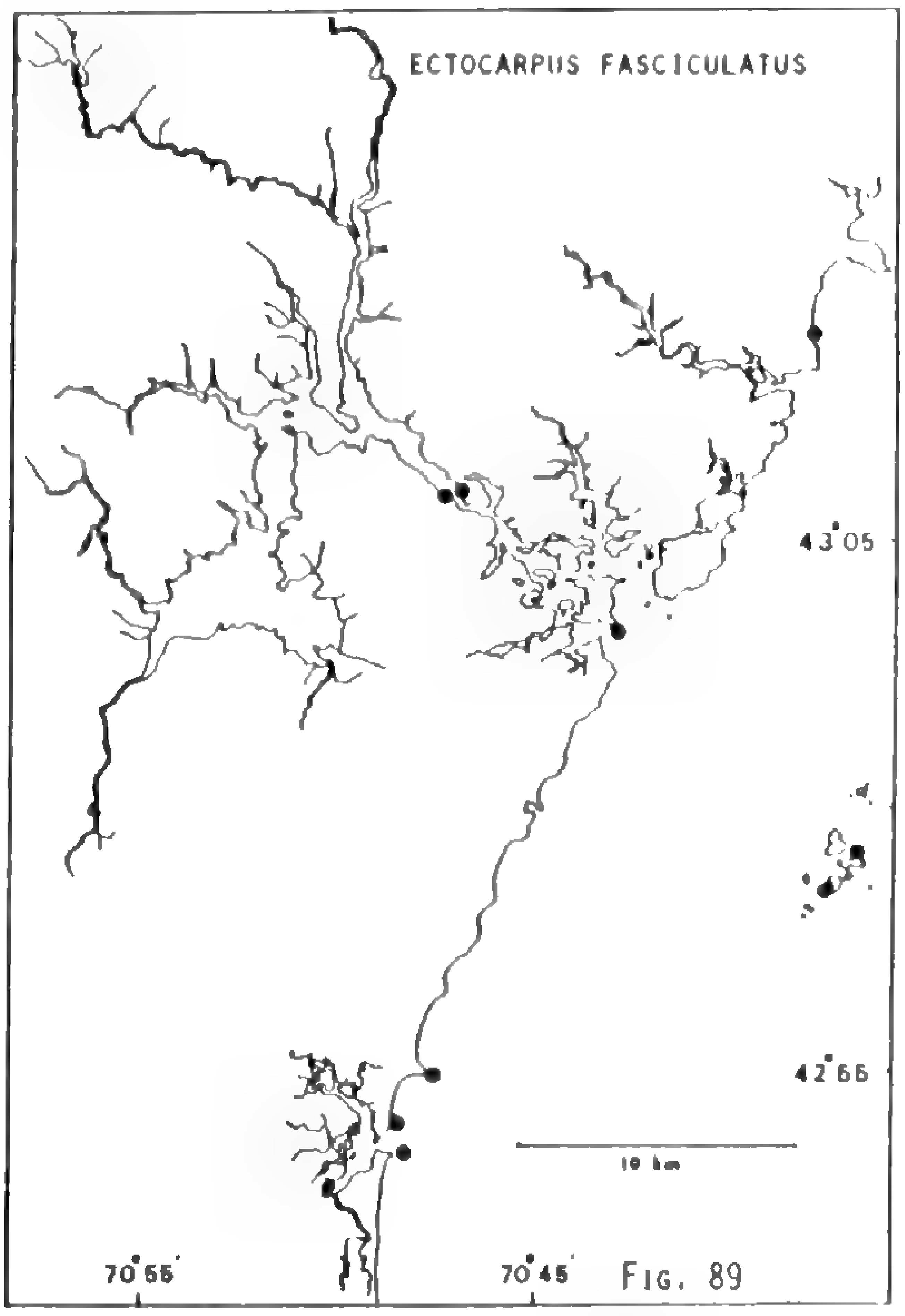

ECTOCARPUS FASCICULATUS

FIG. 89

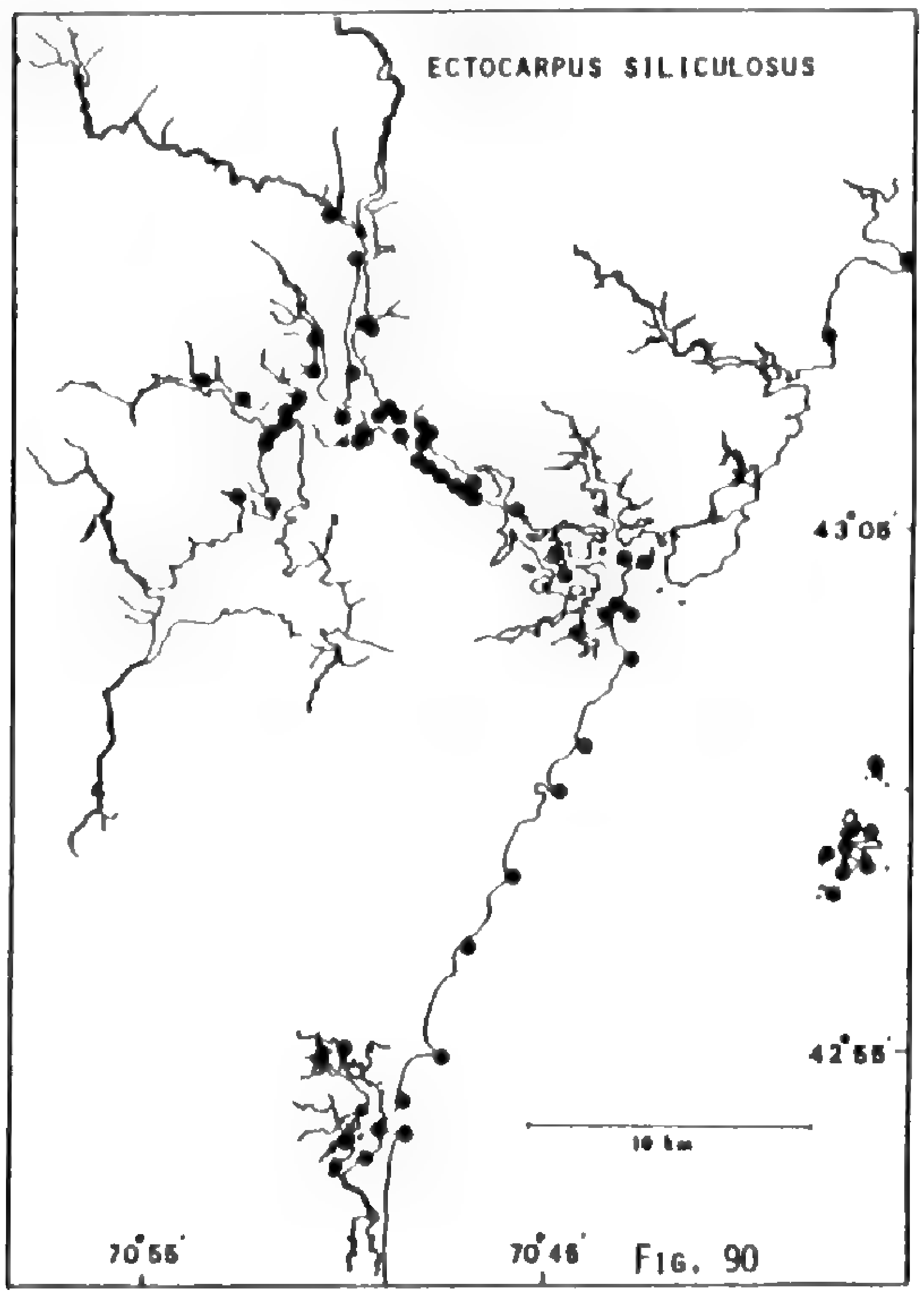

ECTOCARPUS SILICULOSUS

FIG. 90

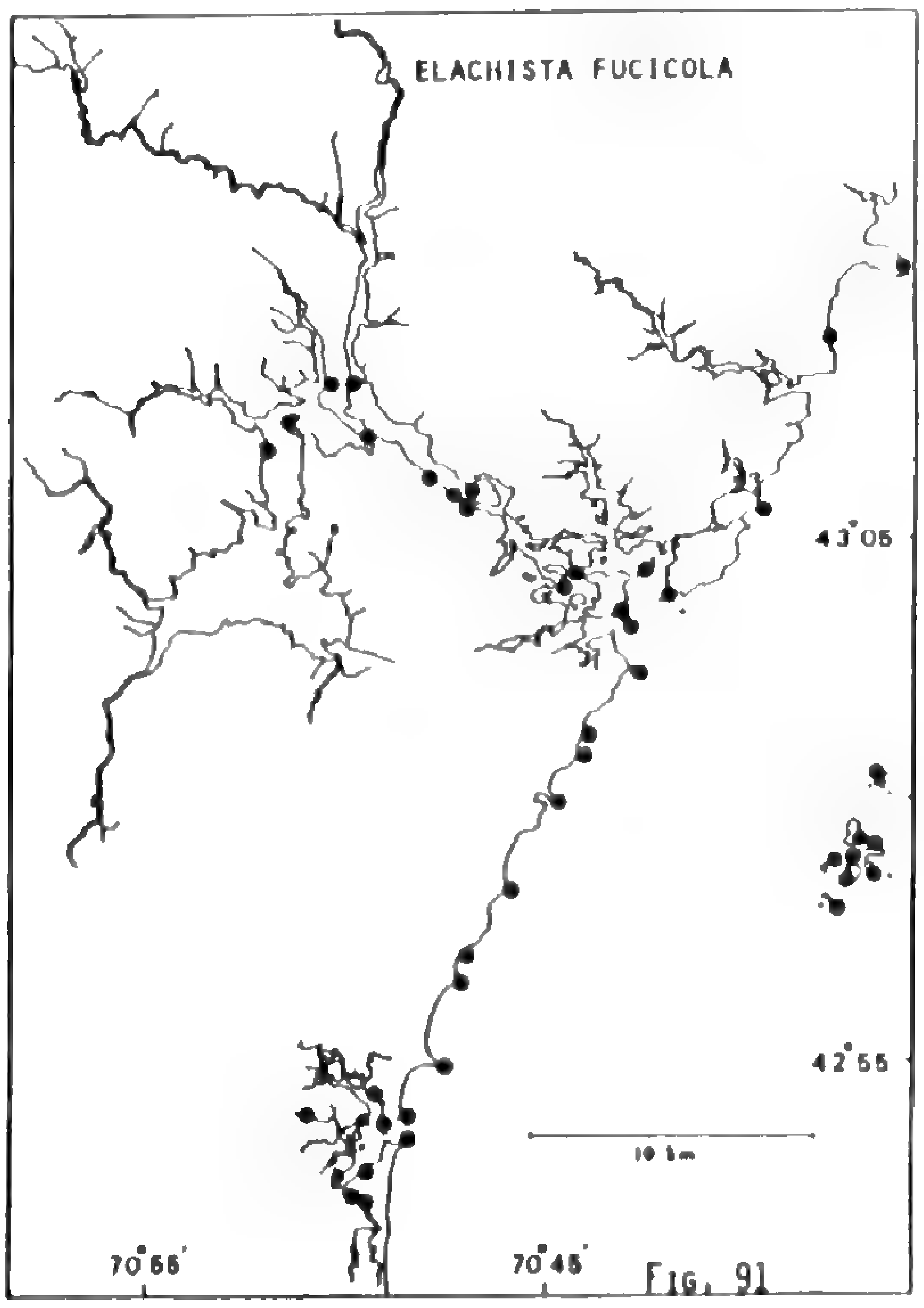

ELACHISTA FUCICOLA

FIG. 91

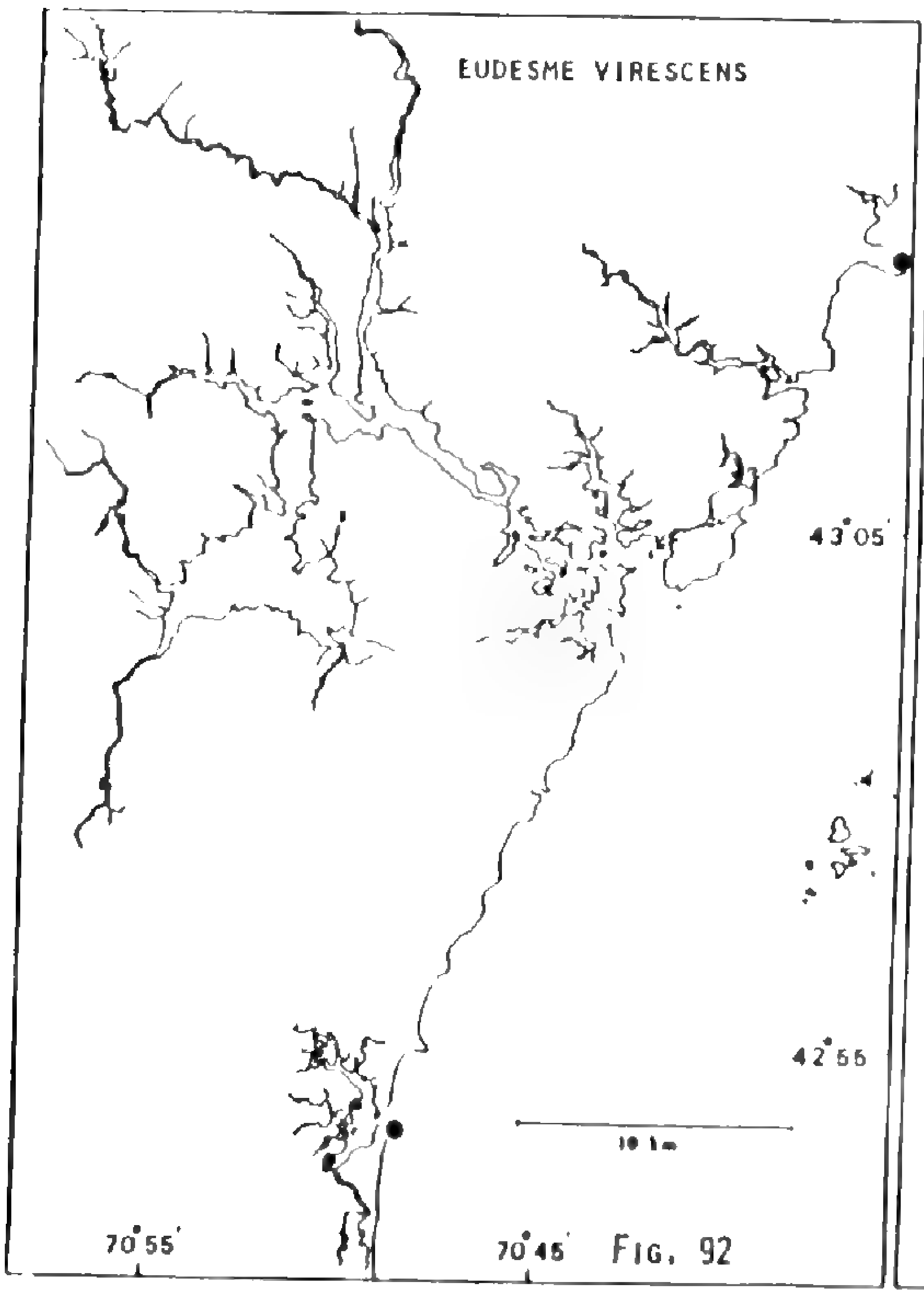


FIG. 92

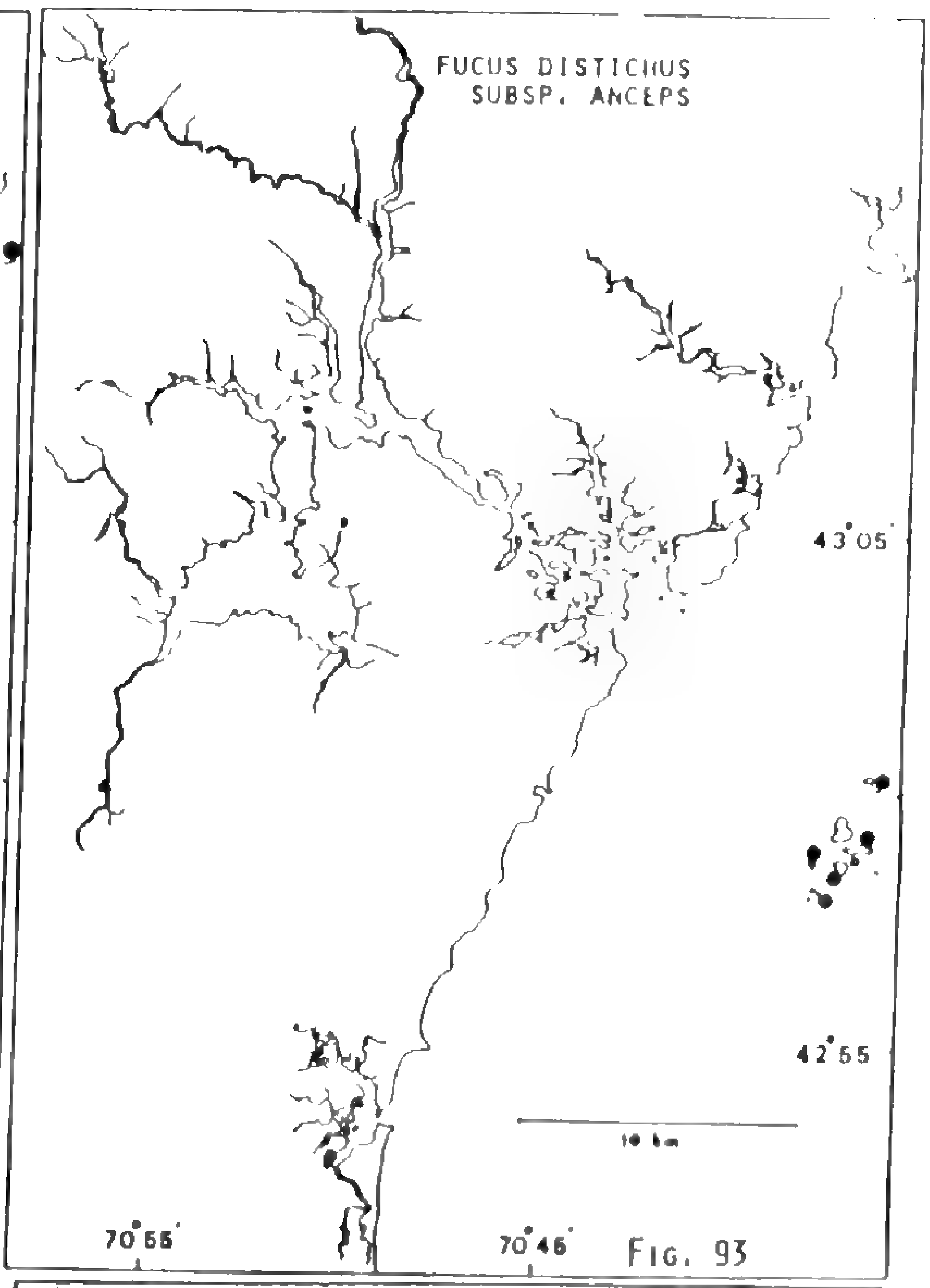


FIG. 93

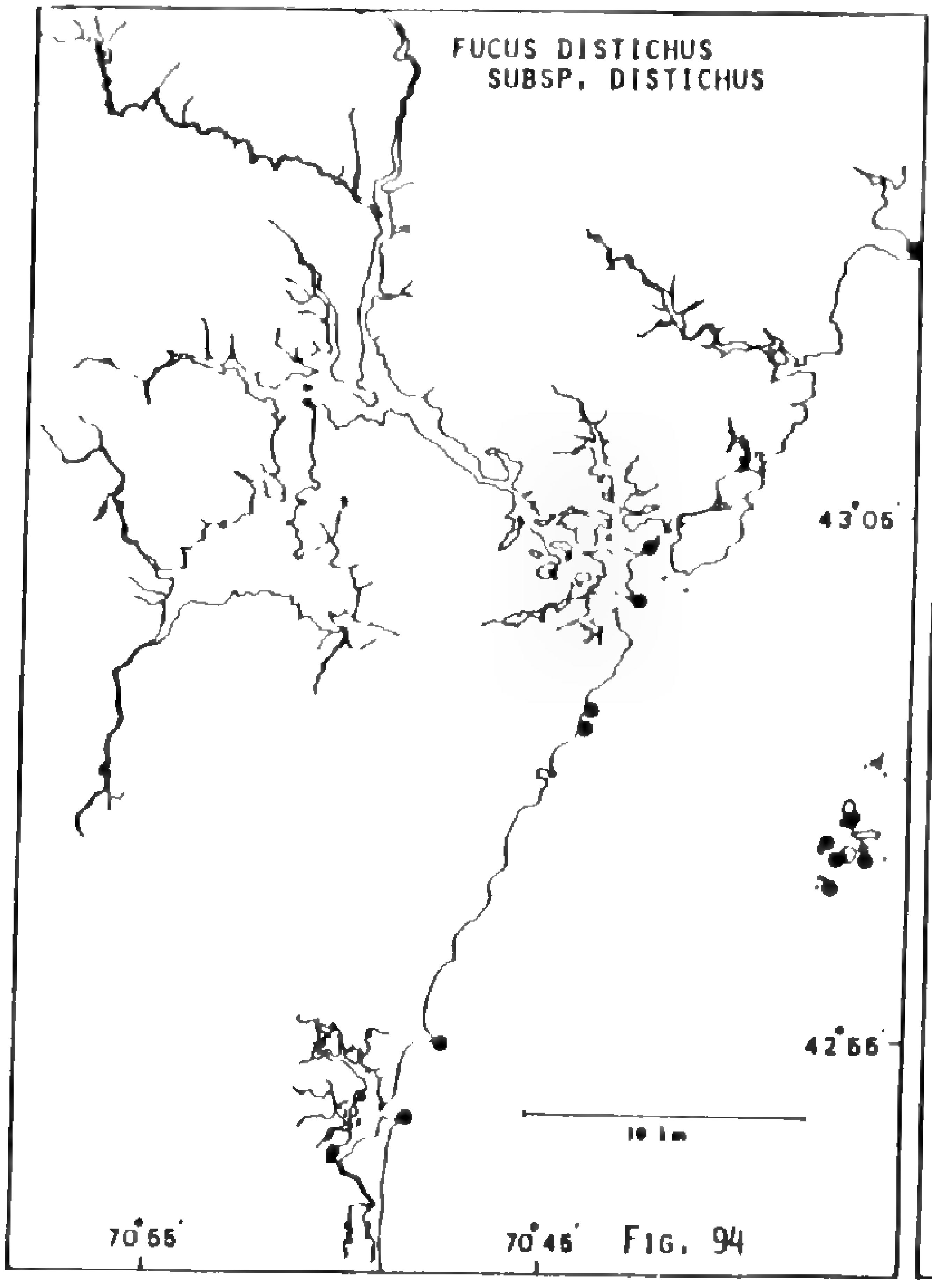


FIG. 94

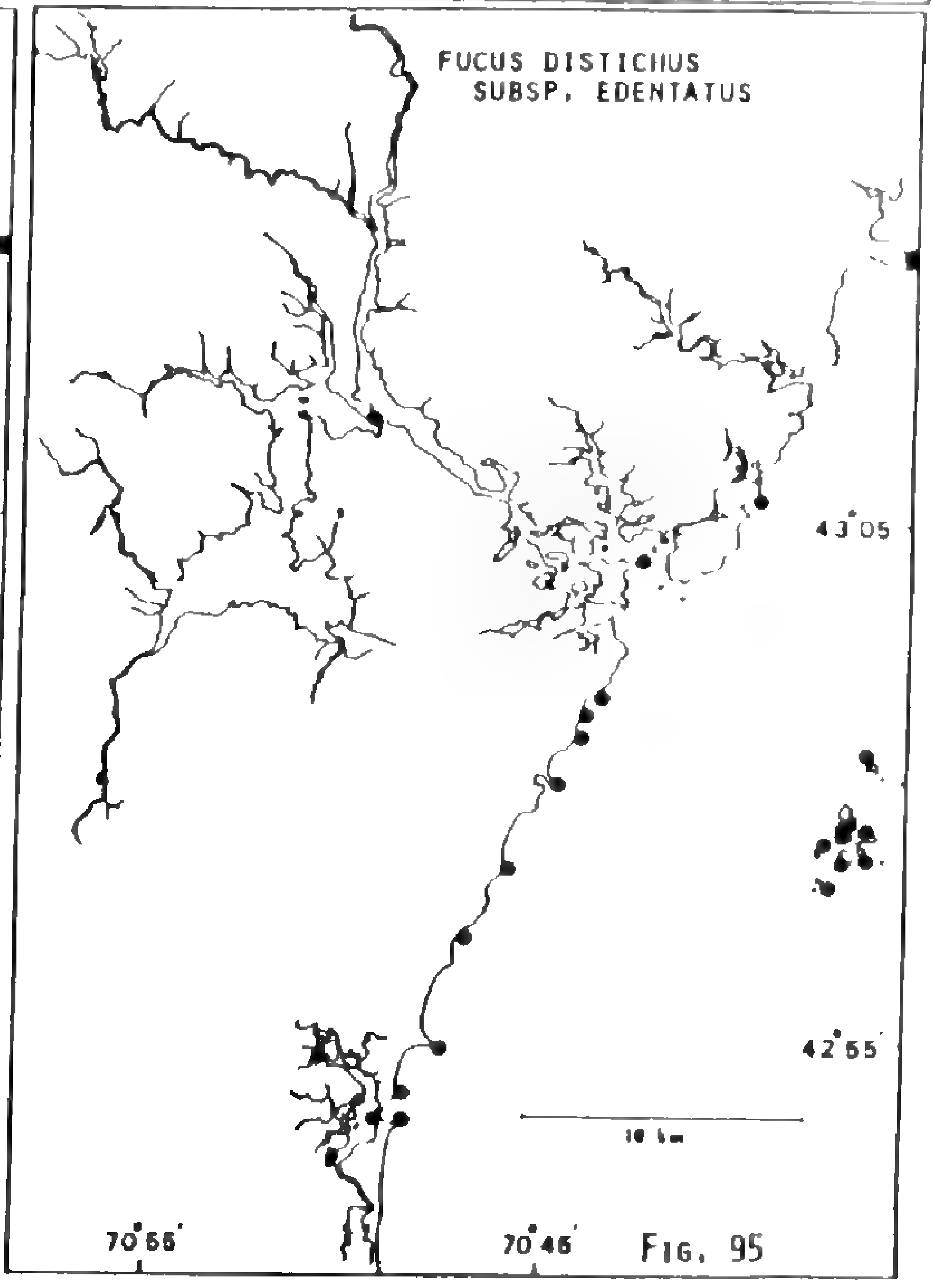


FIG. 95

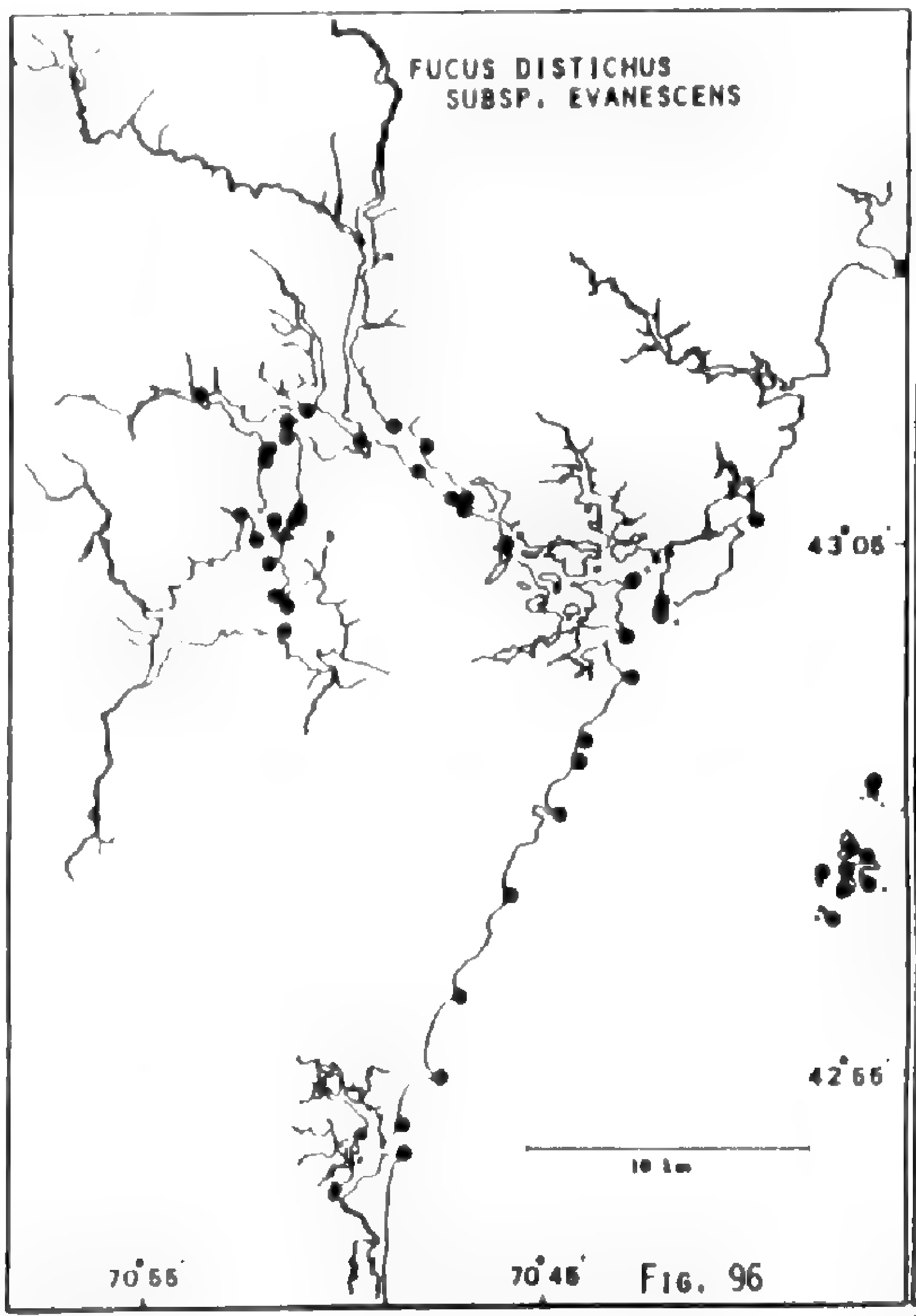


FIG. 96

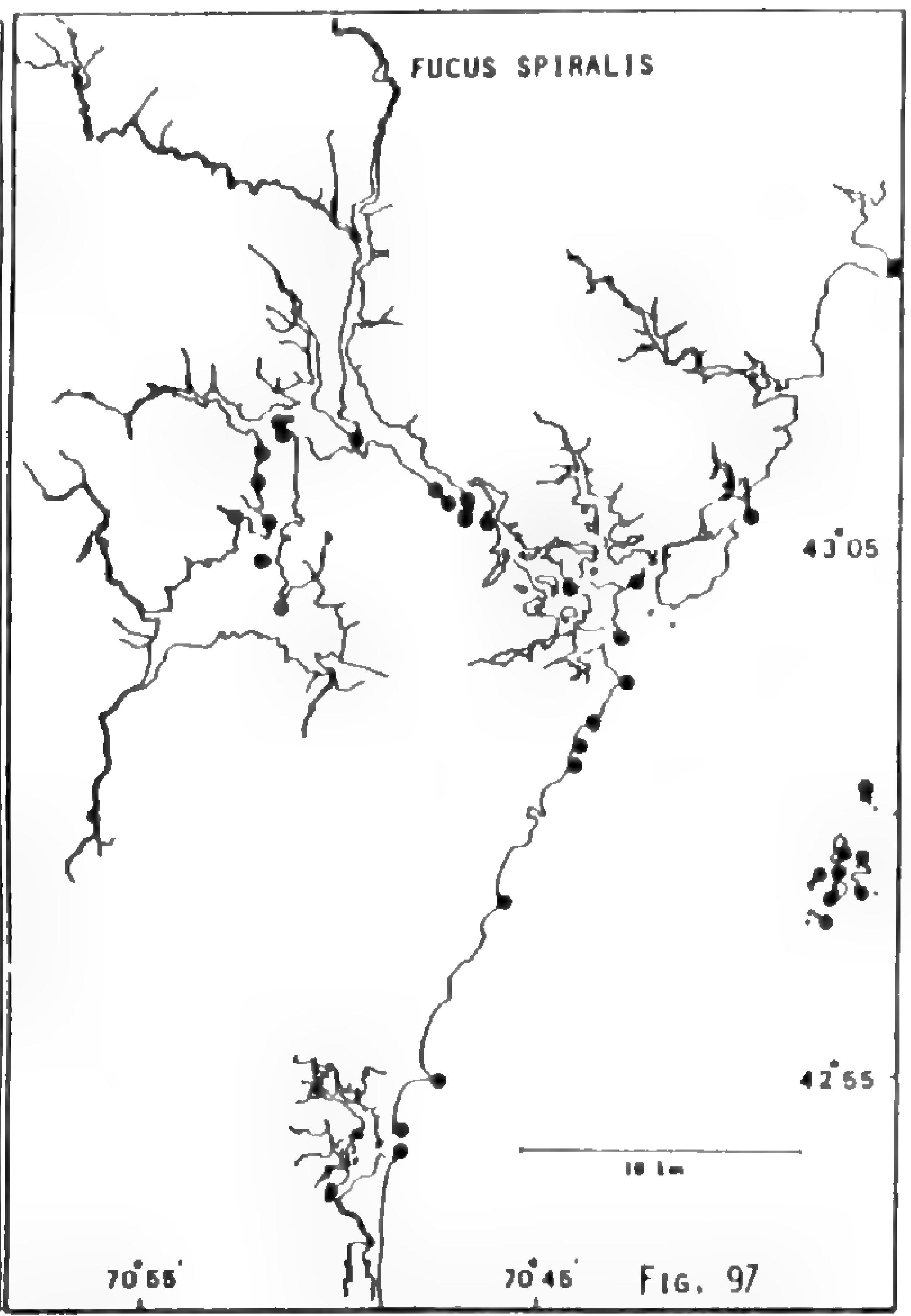


FIG. 97

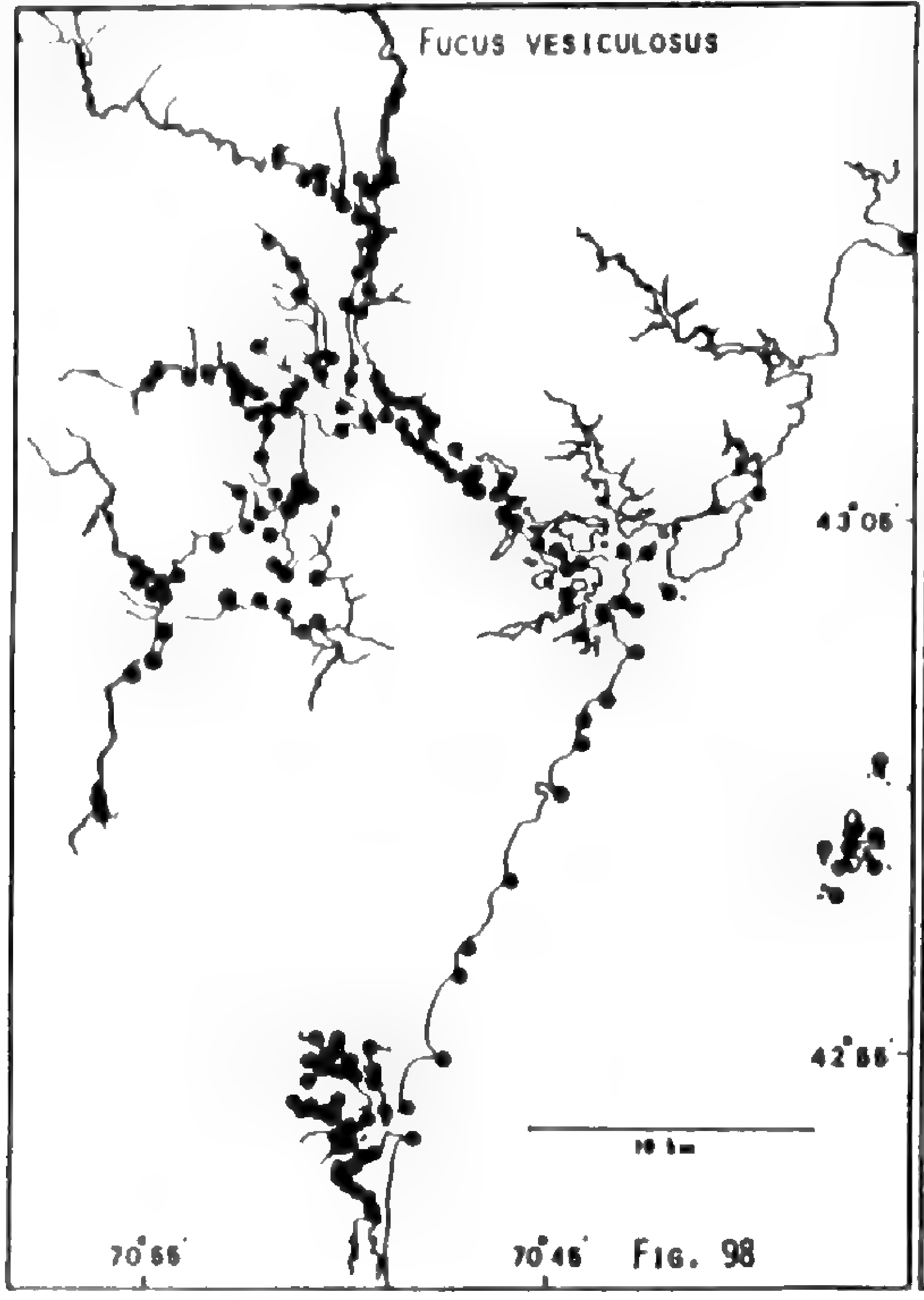


FIG. 98

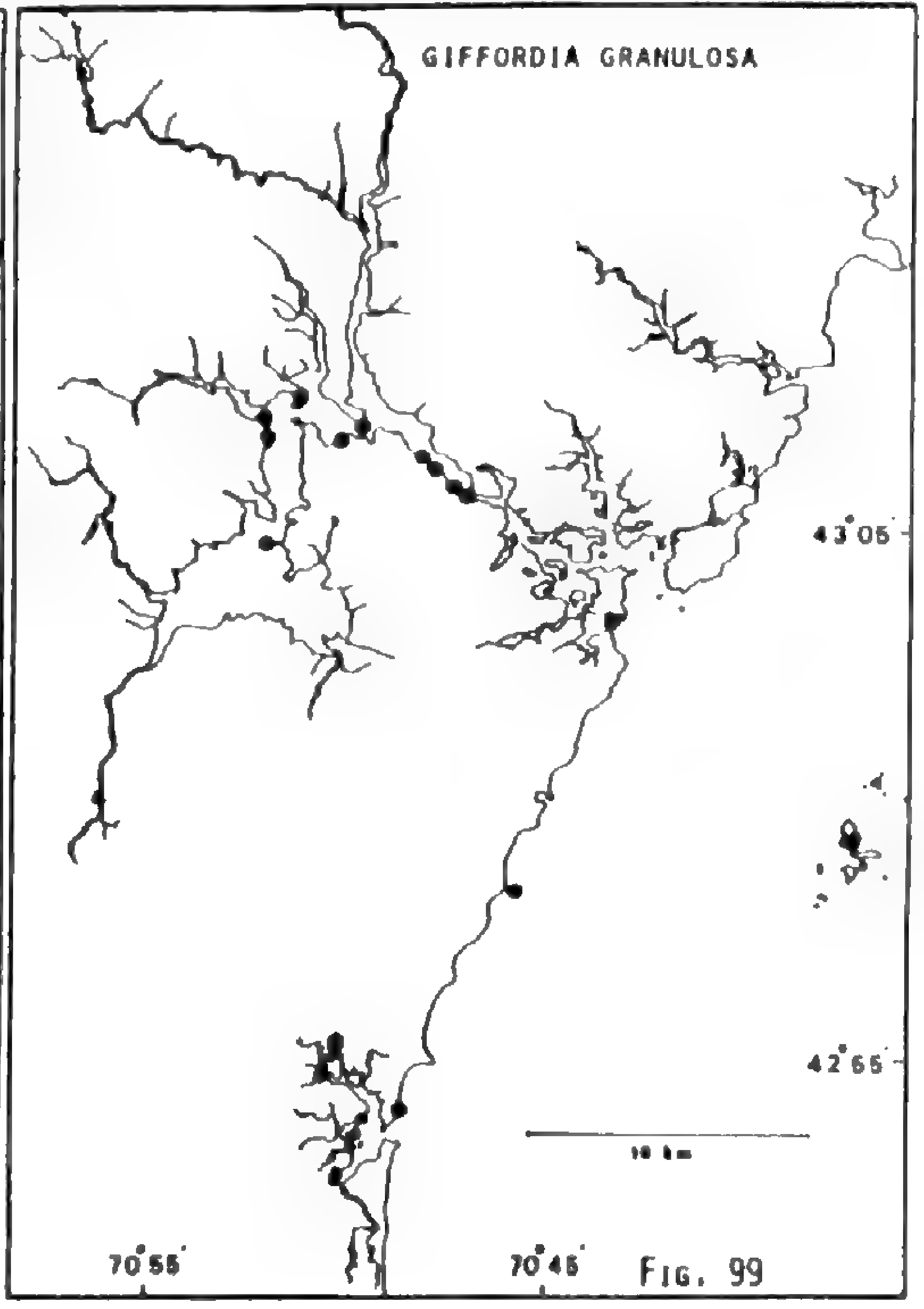


FIG. 99

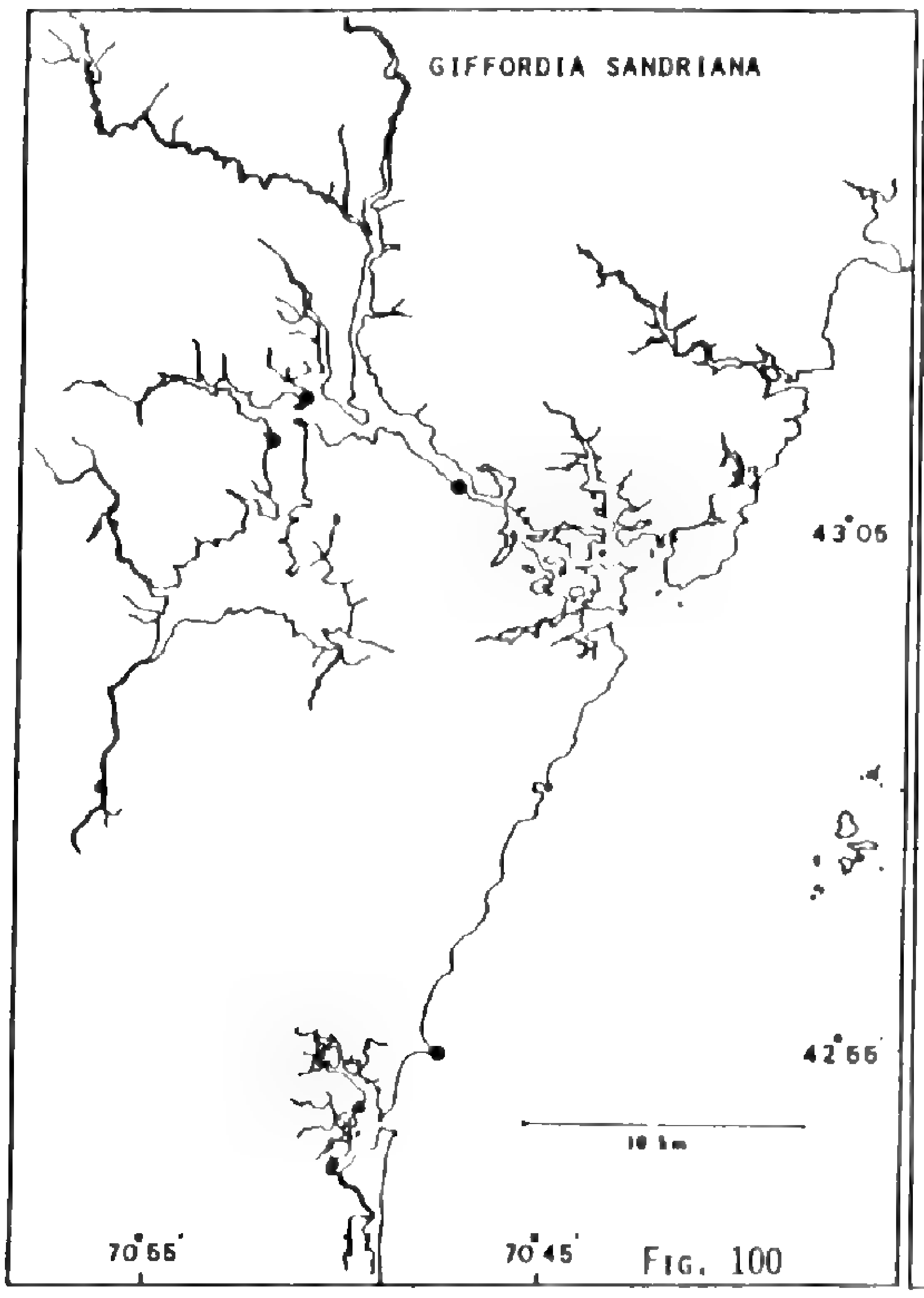


FIG. 100

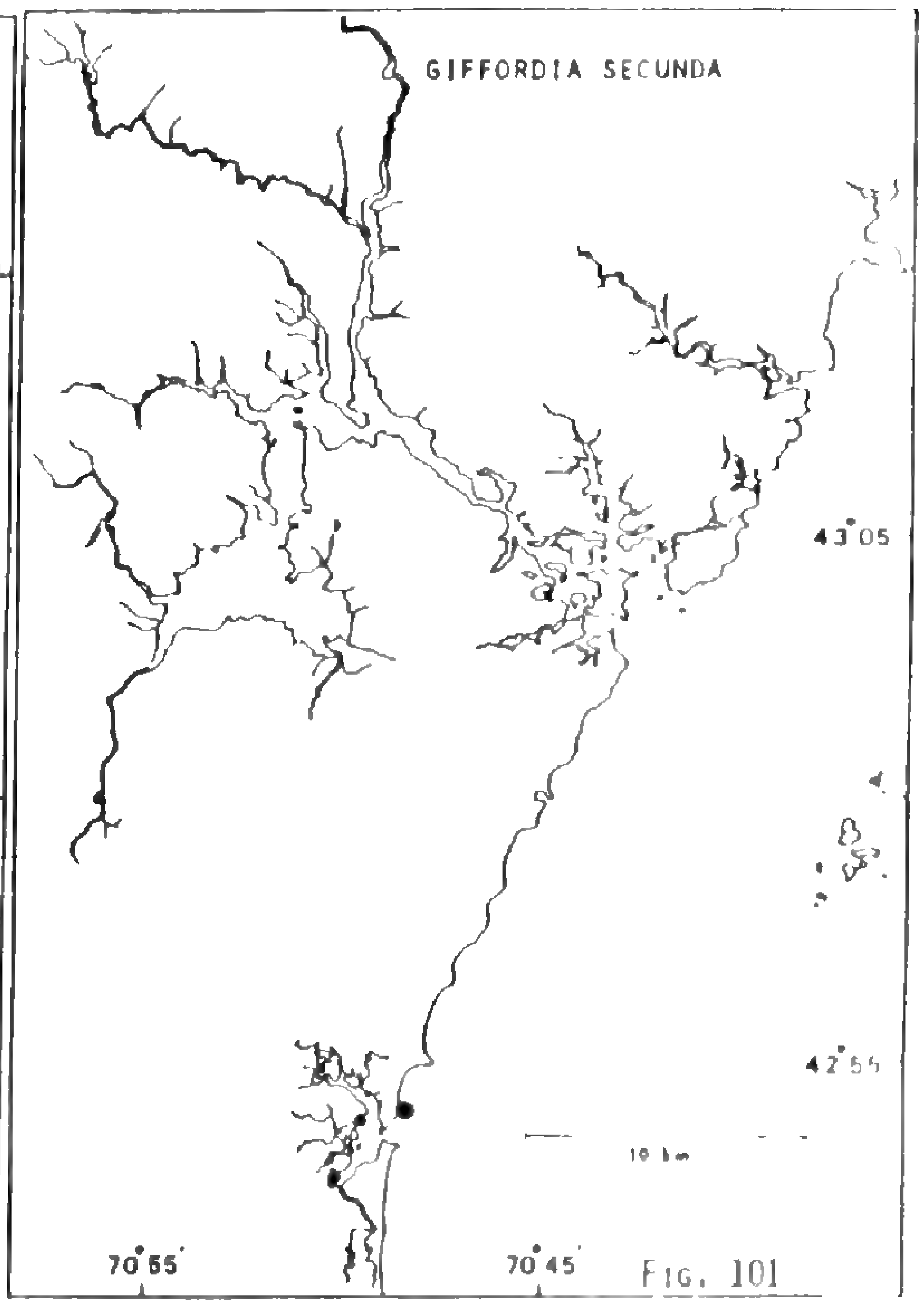


FIG. 101

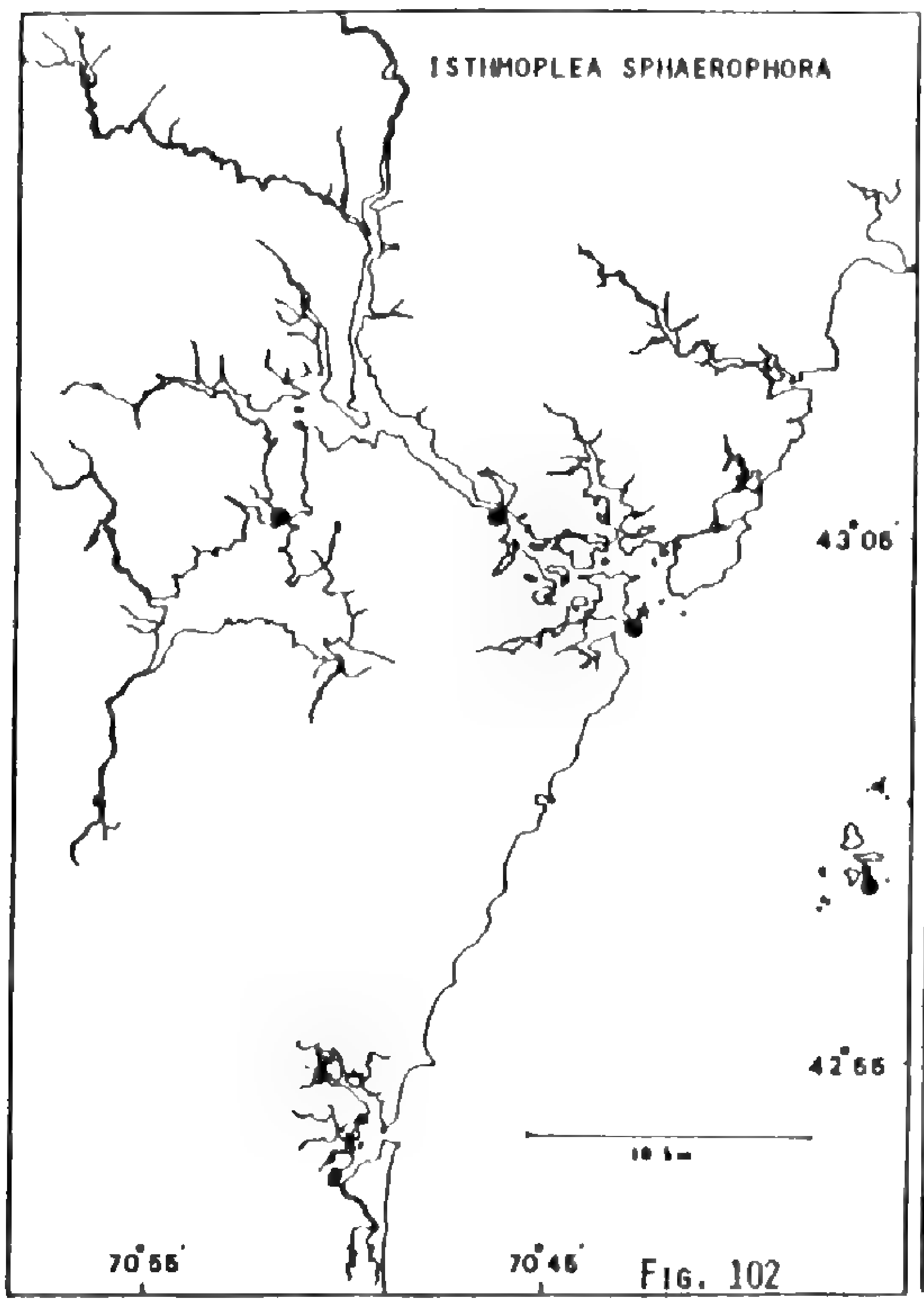


FIG. 102

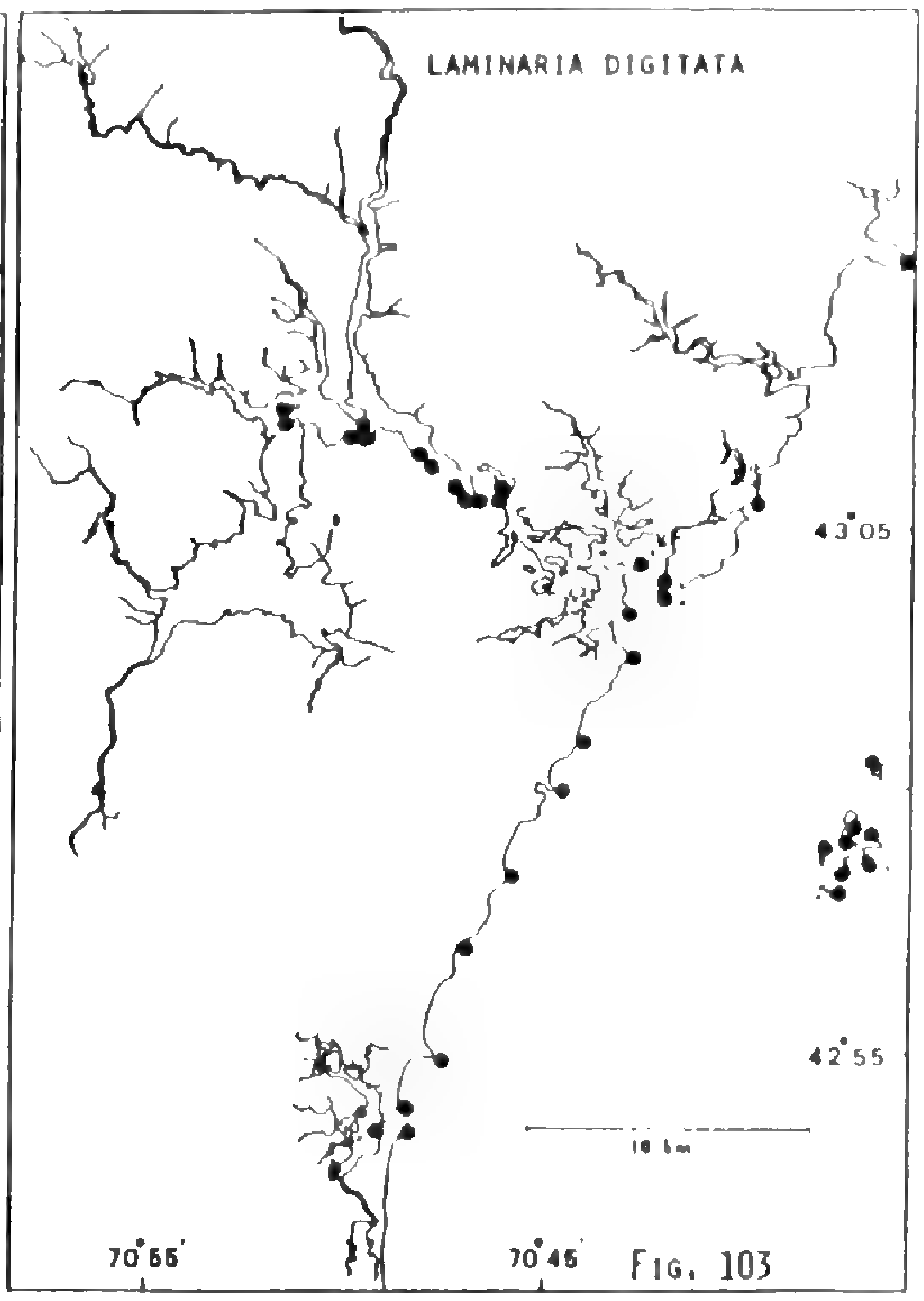


FIG. 103

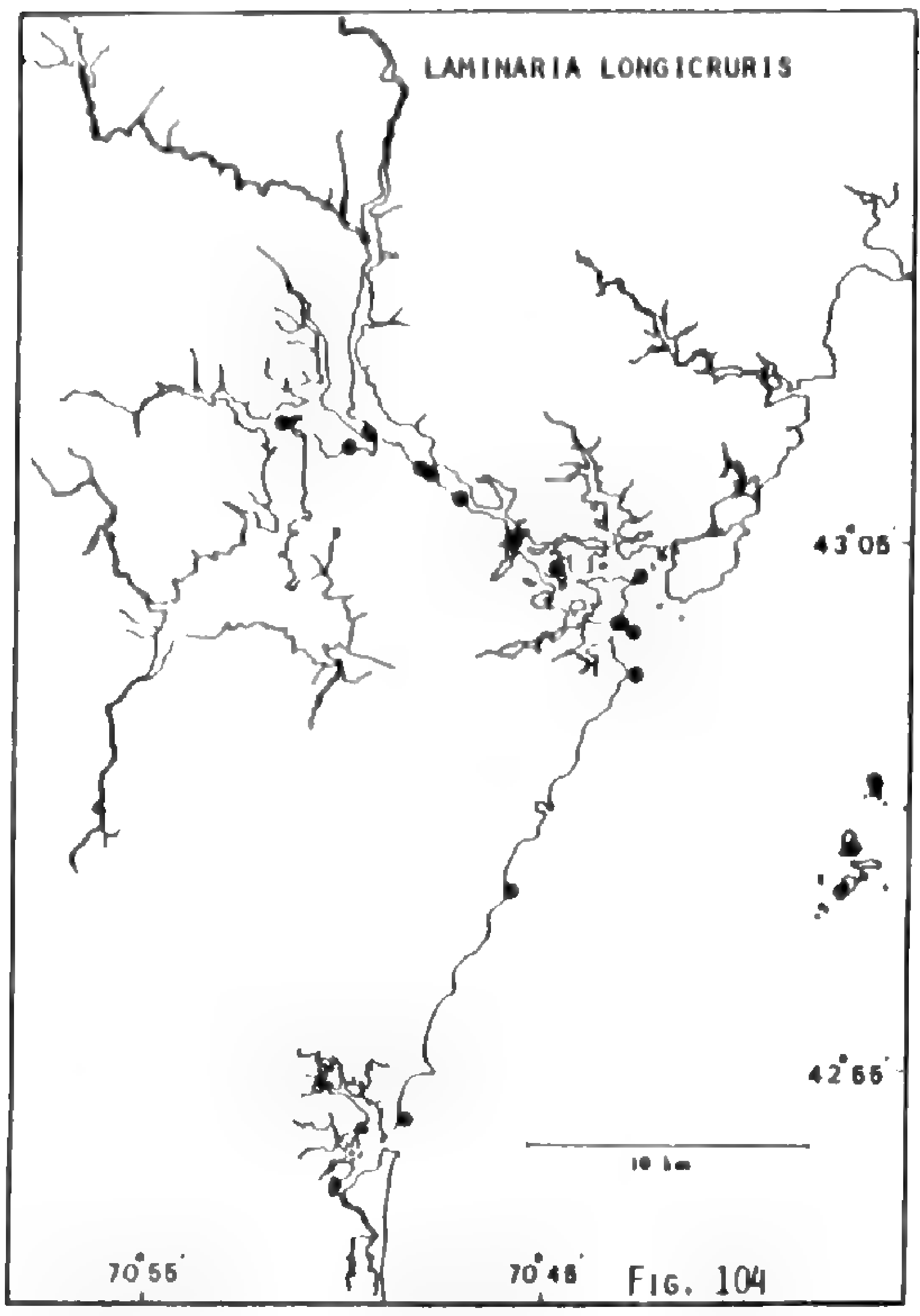

LAMINARIA LONGICRURIS

FIG. 104

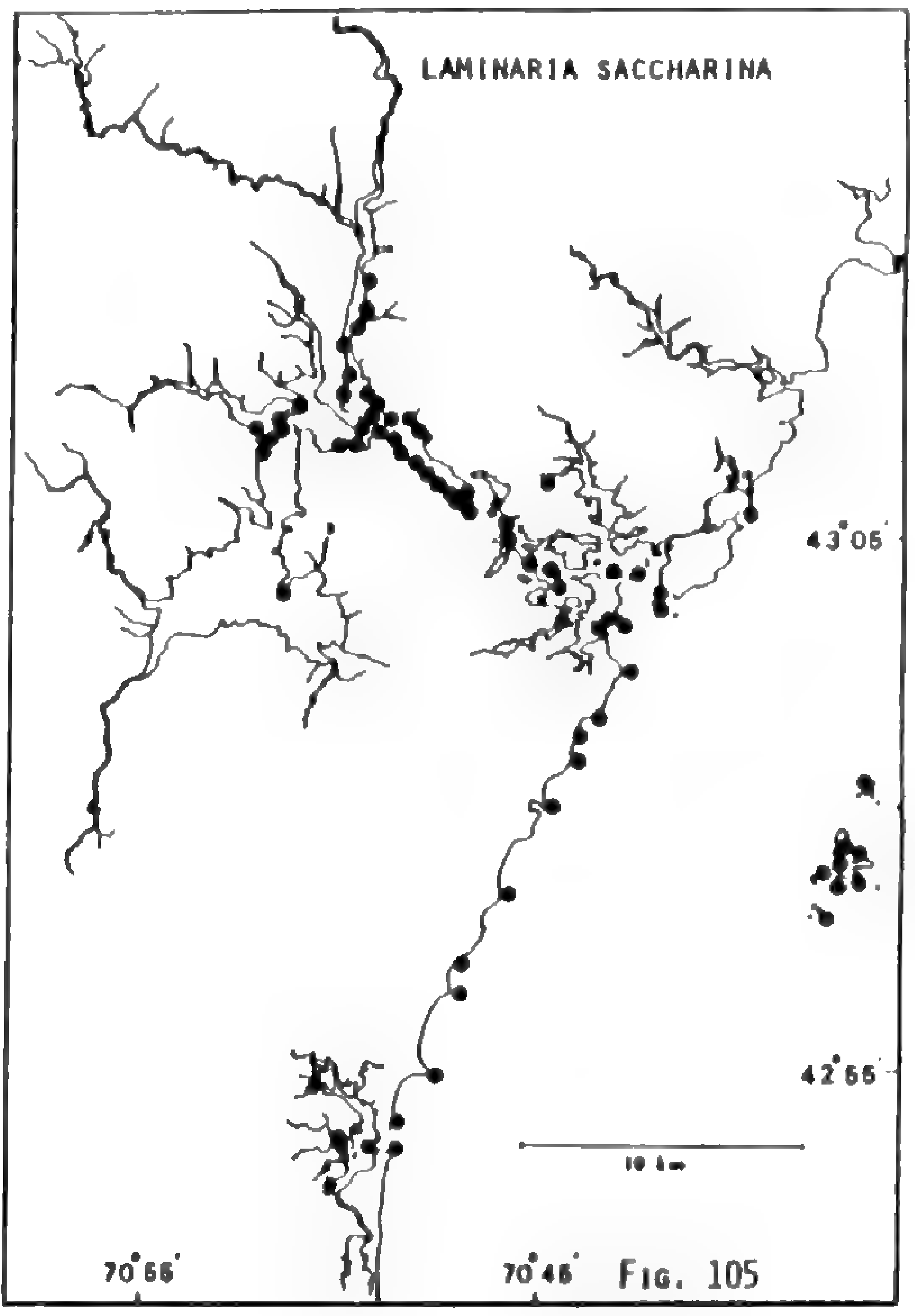

LAMINARIA SACCHARINA

FIG. 105

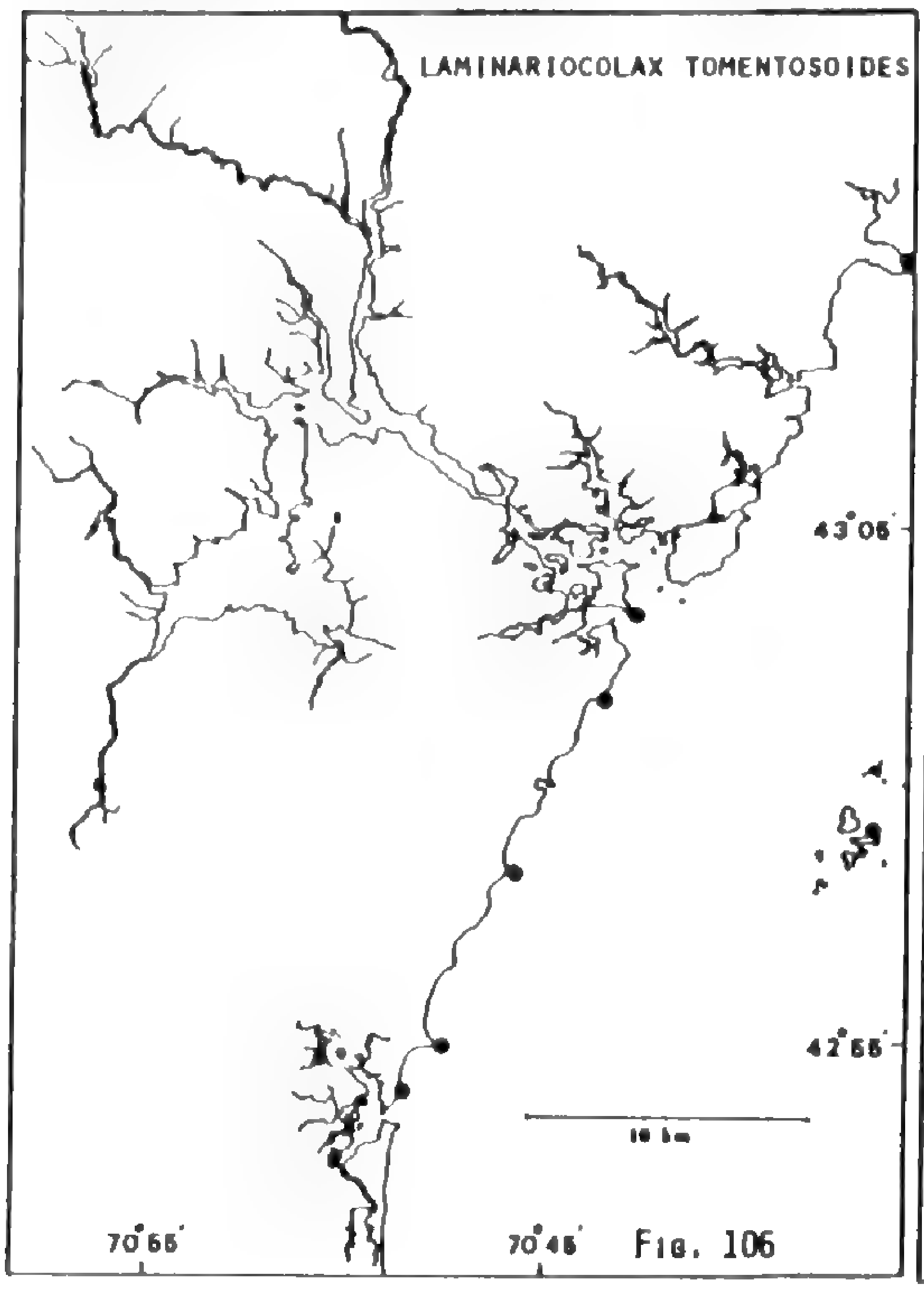

LAMINARIOCOLAX TOMENTOSOIDES

FIG. 106

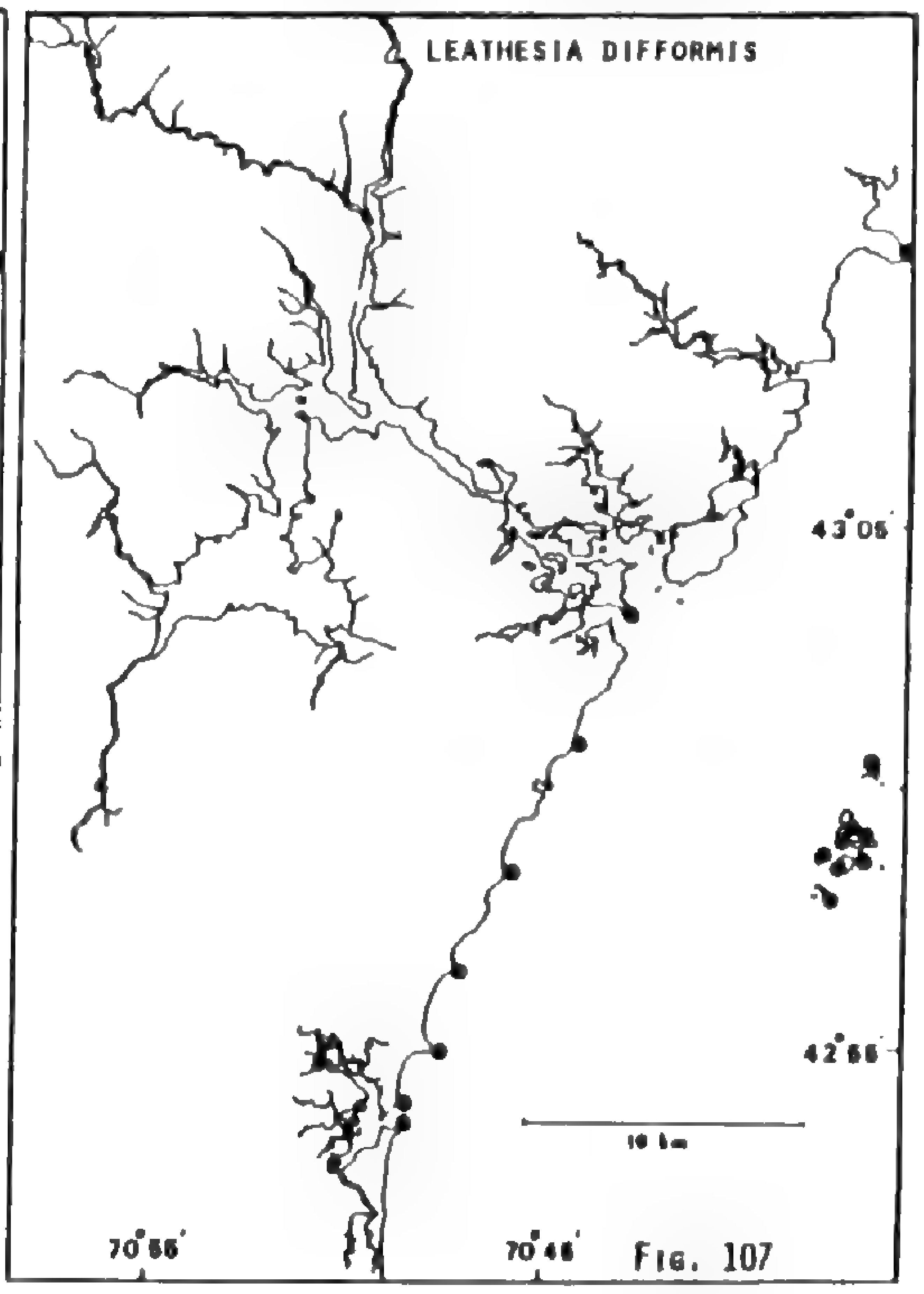

LEATHESIA DIFFORMIS

FIG. 107

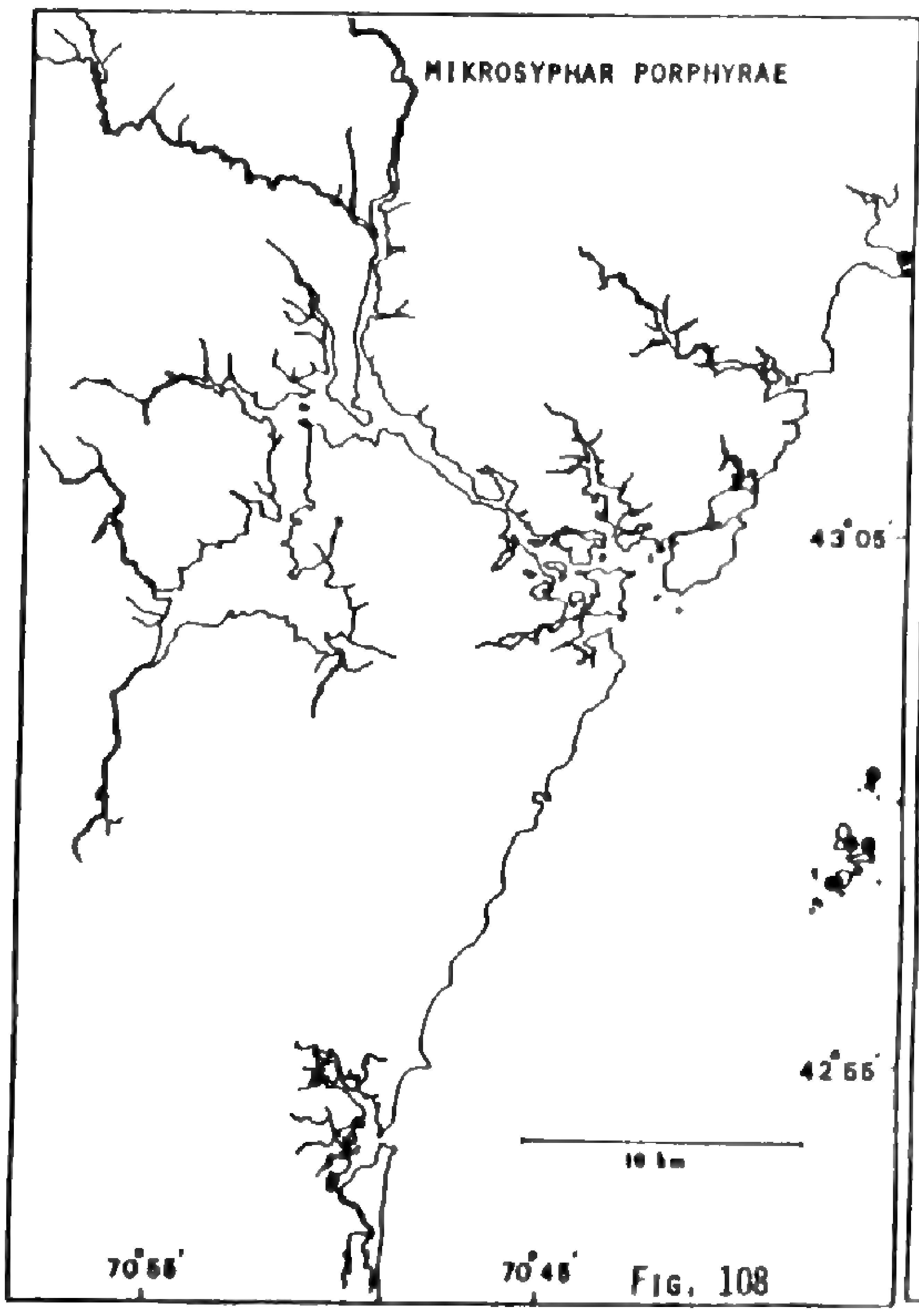


Fig. 108

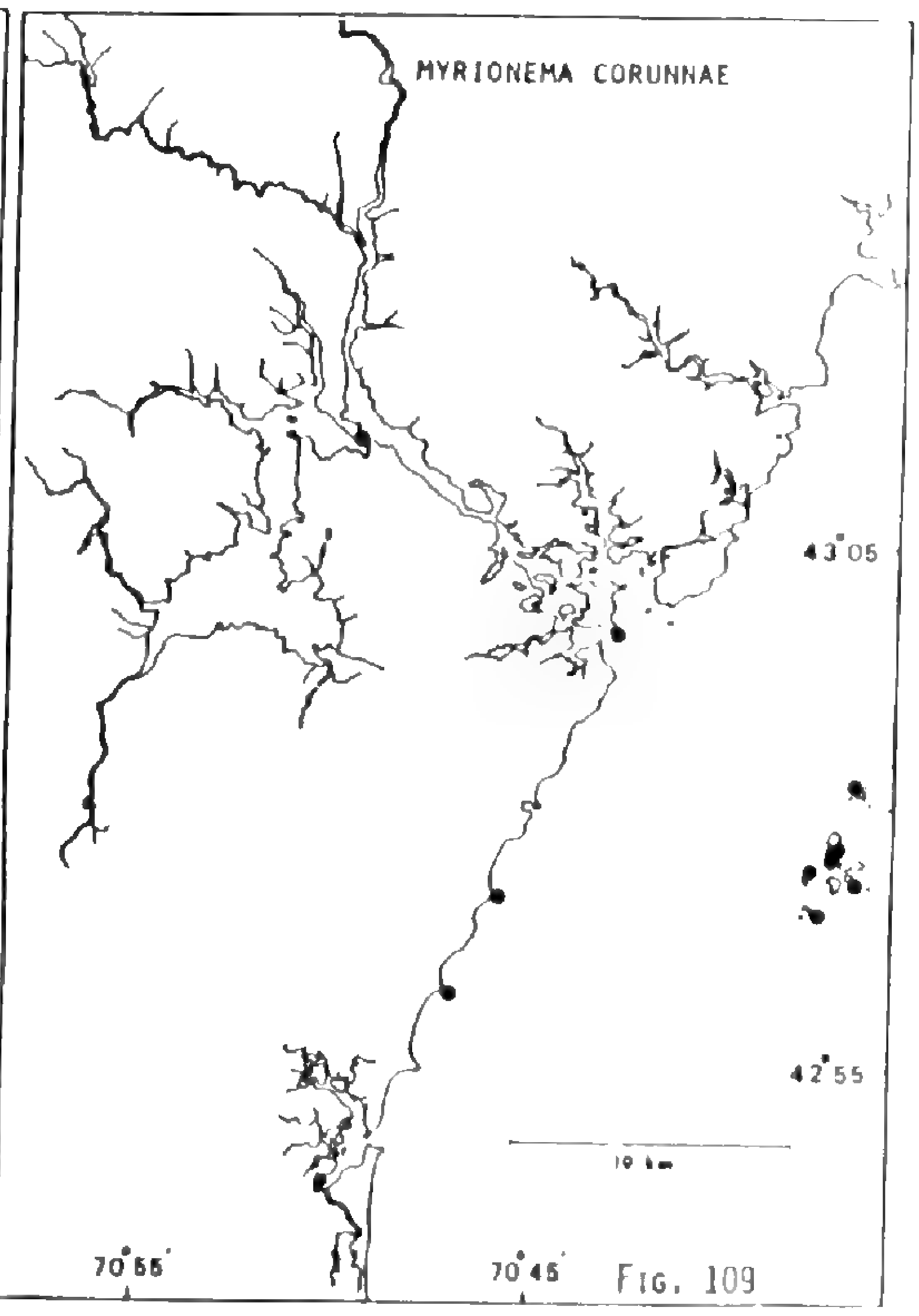


Fig. 109

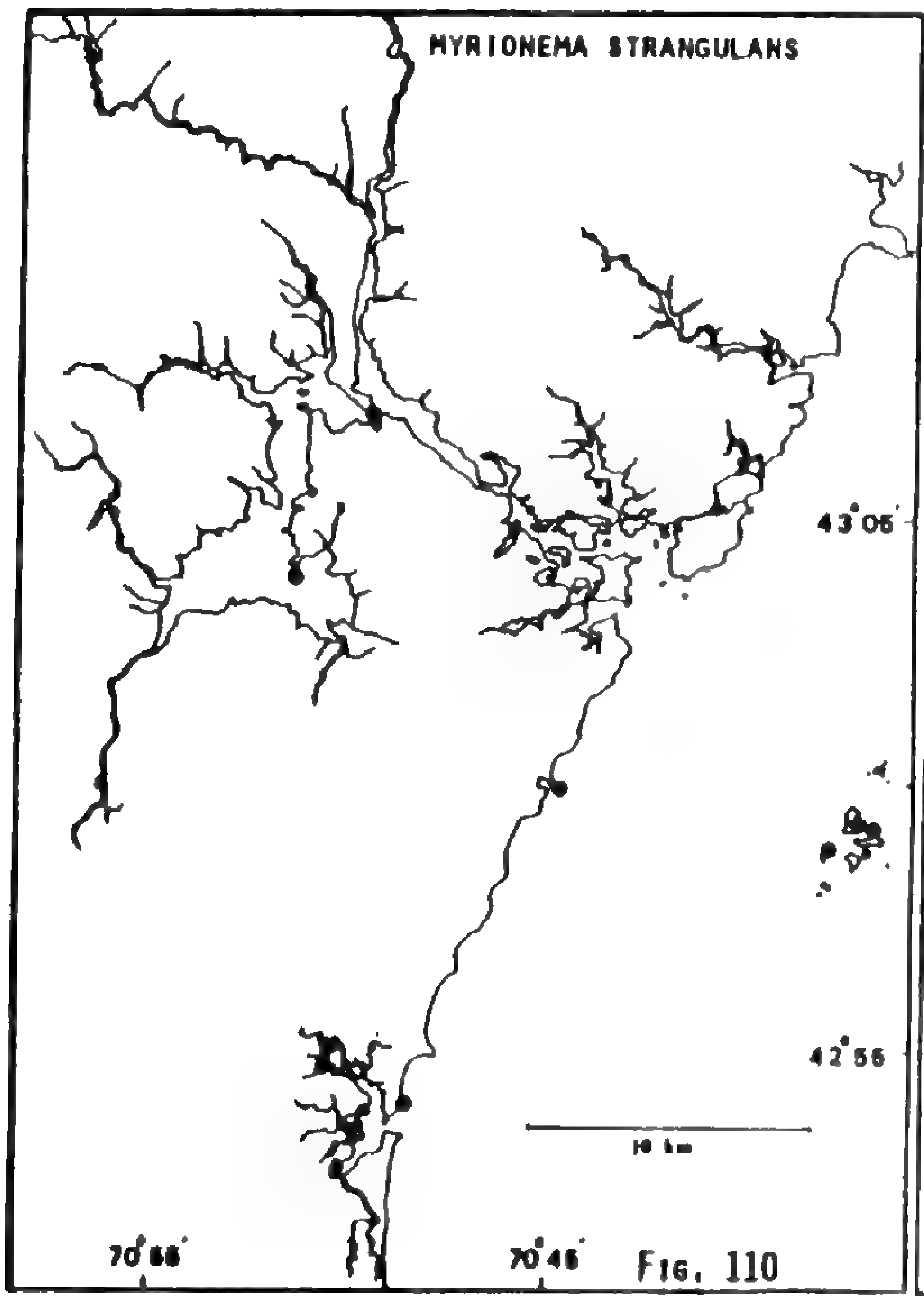


Fig. 110

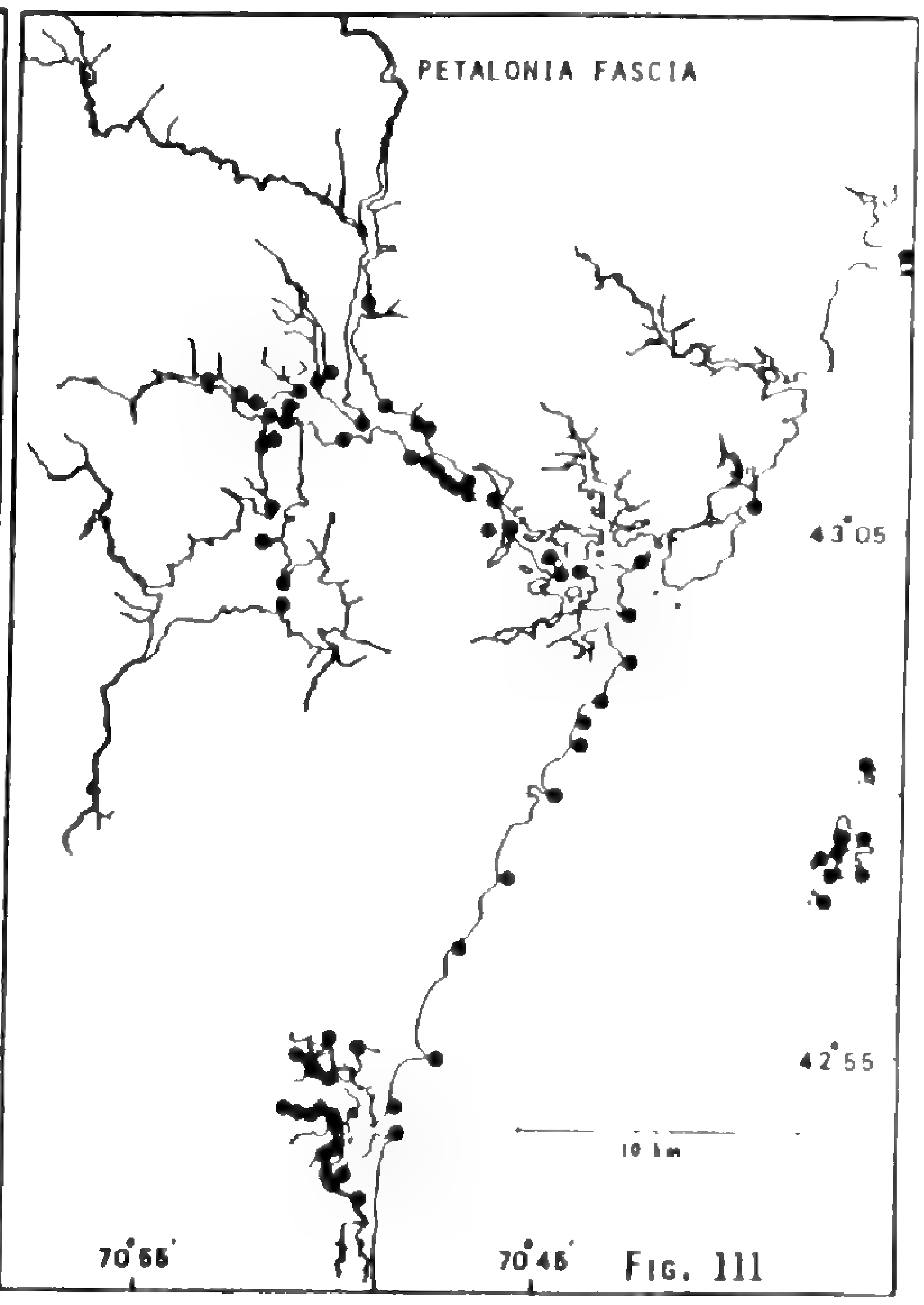


Fig. 111

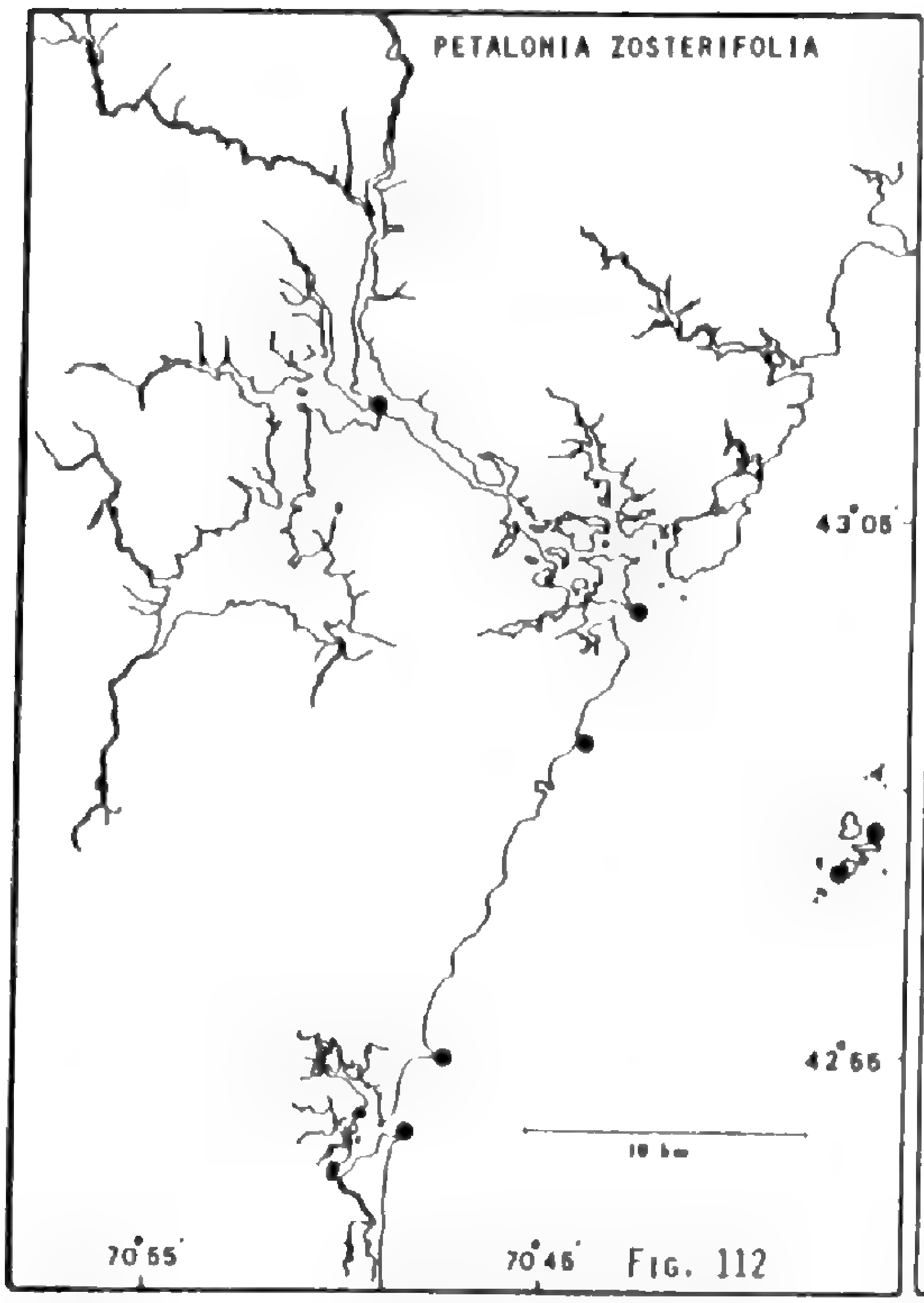

PETALONIA ZOSTERIFOLIA

FIG. 112

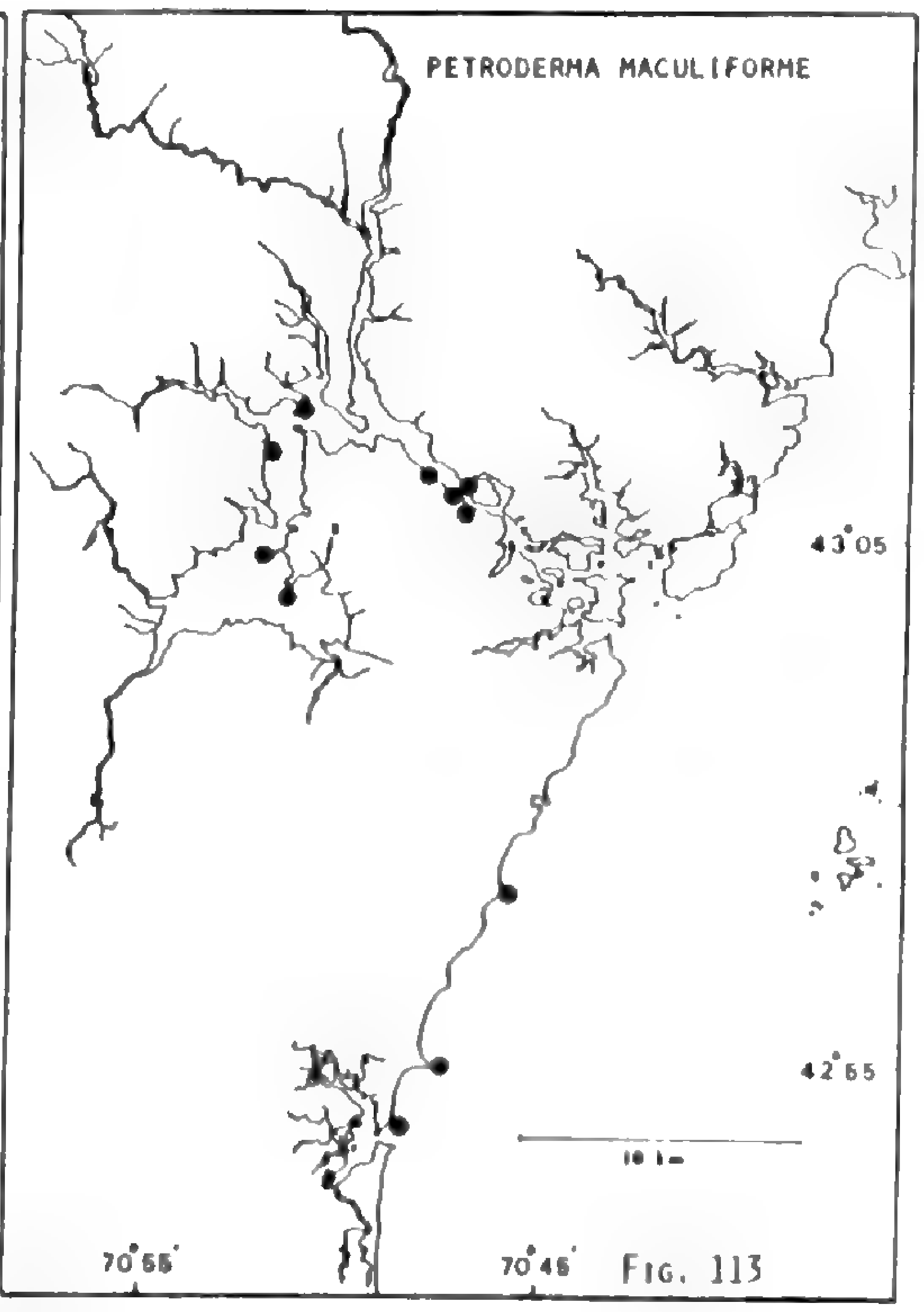

PETRODERMA MACULIFORME

FIG. 113

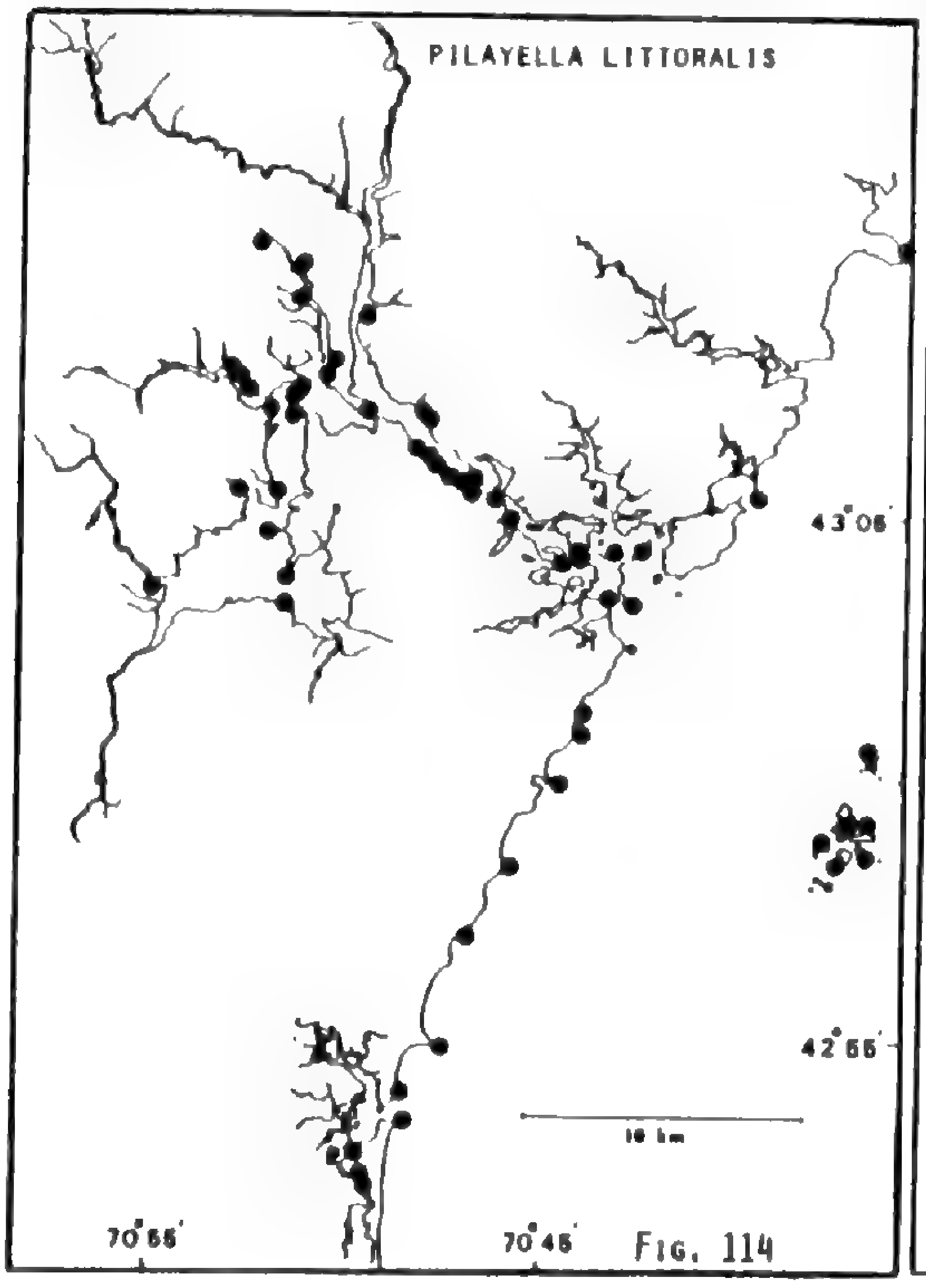

PILAYELLA LITTORALIS

FIG. 114

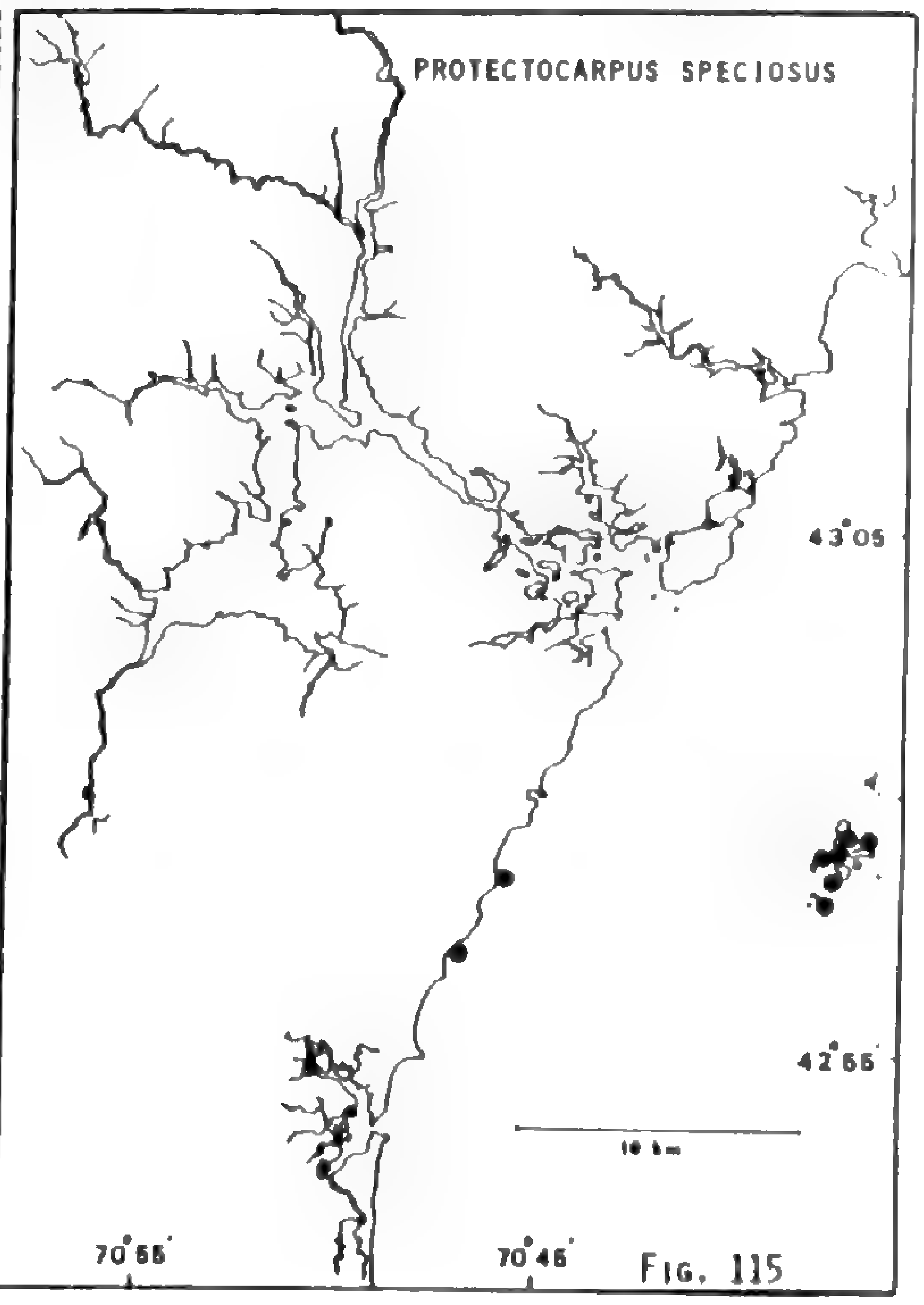

PROTECTOCARPUS SPECIOSUS

FIG. 115

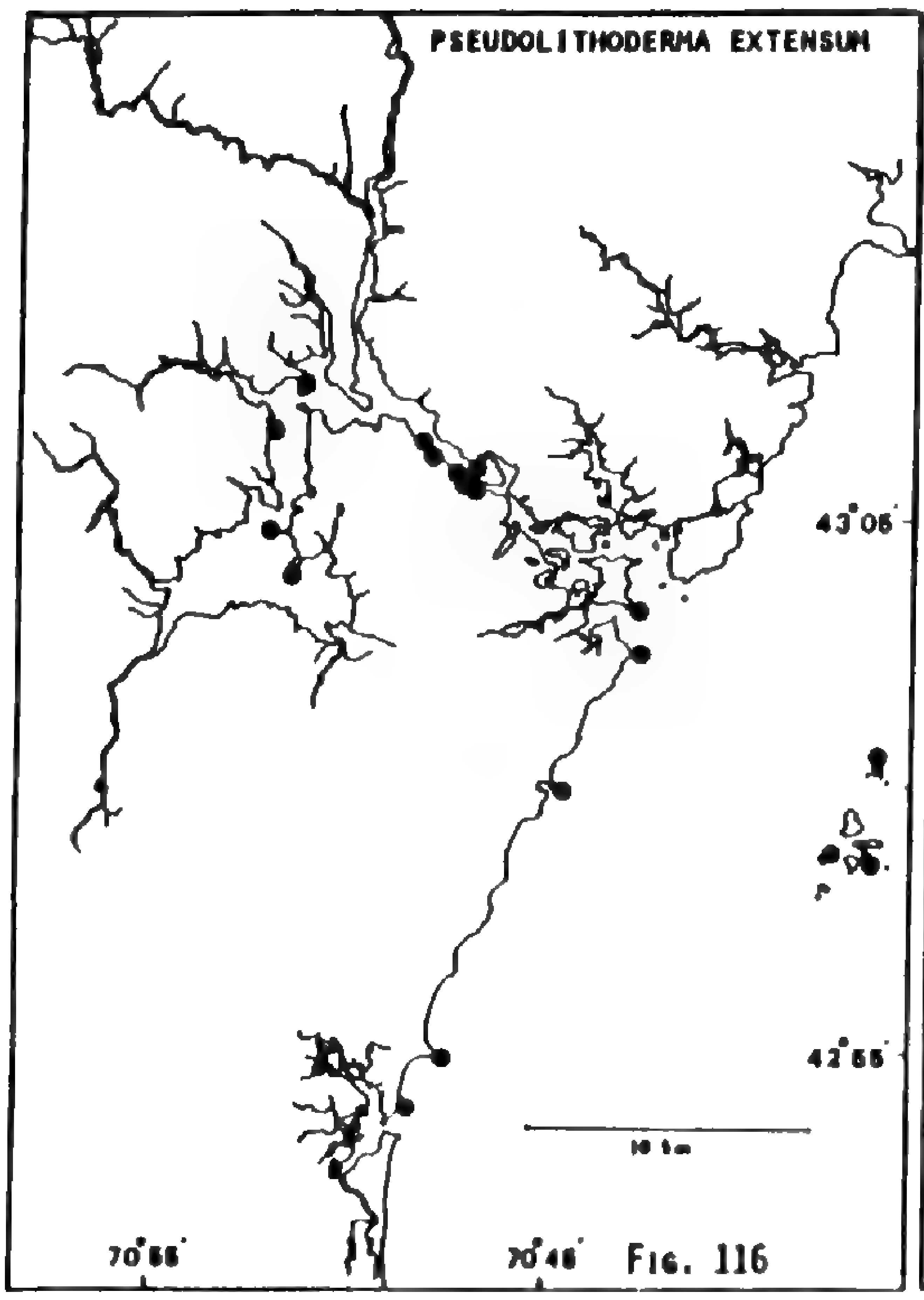


Fig. 116

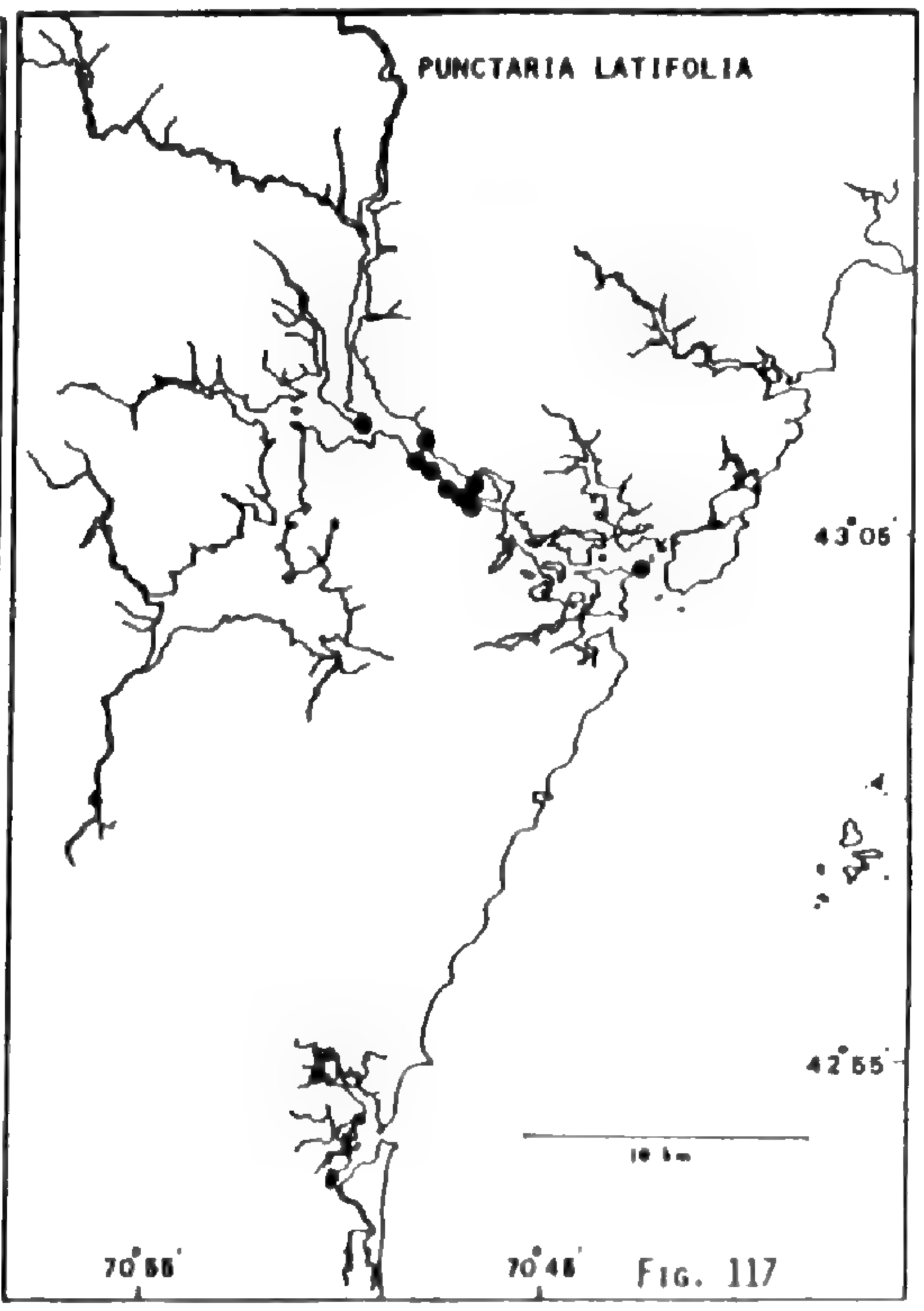


Fig. 117

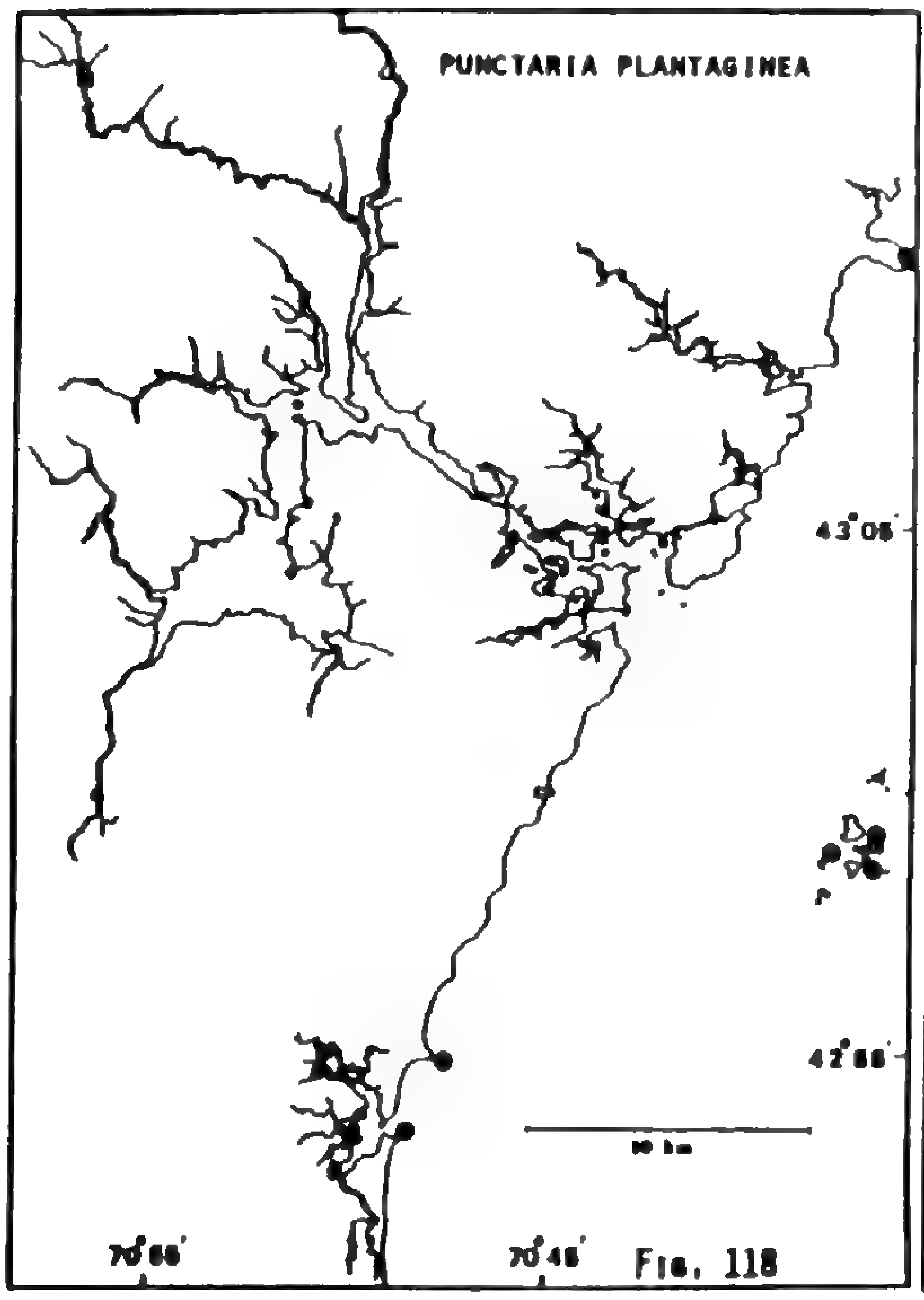


Fig. 118

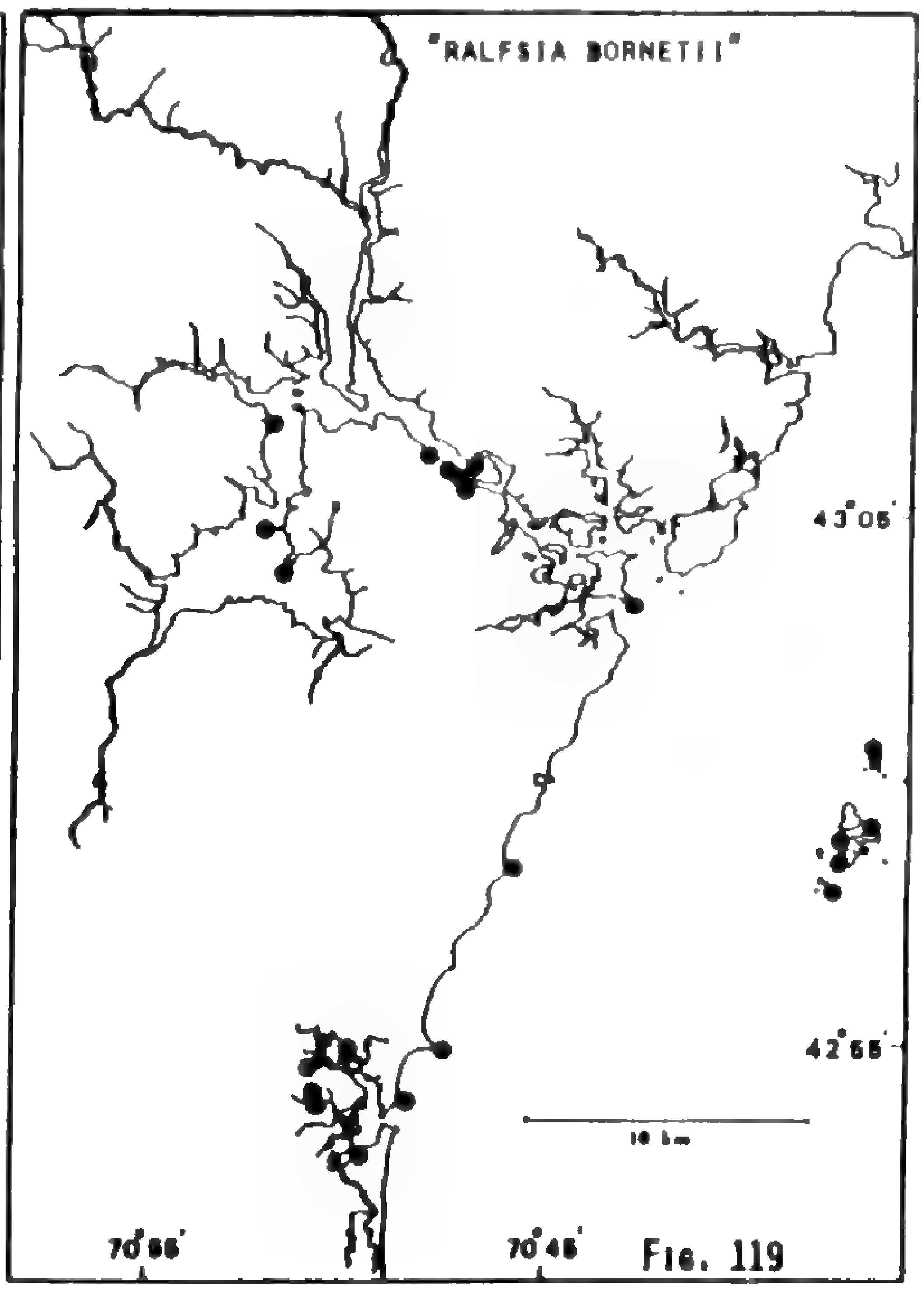


Fig. 119

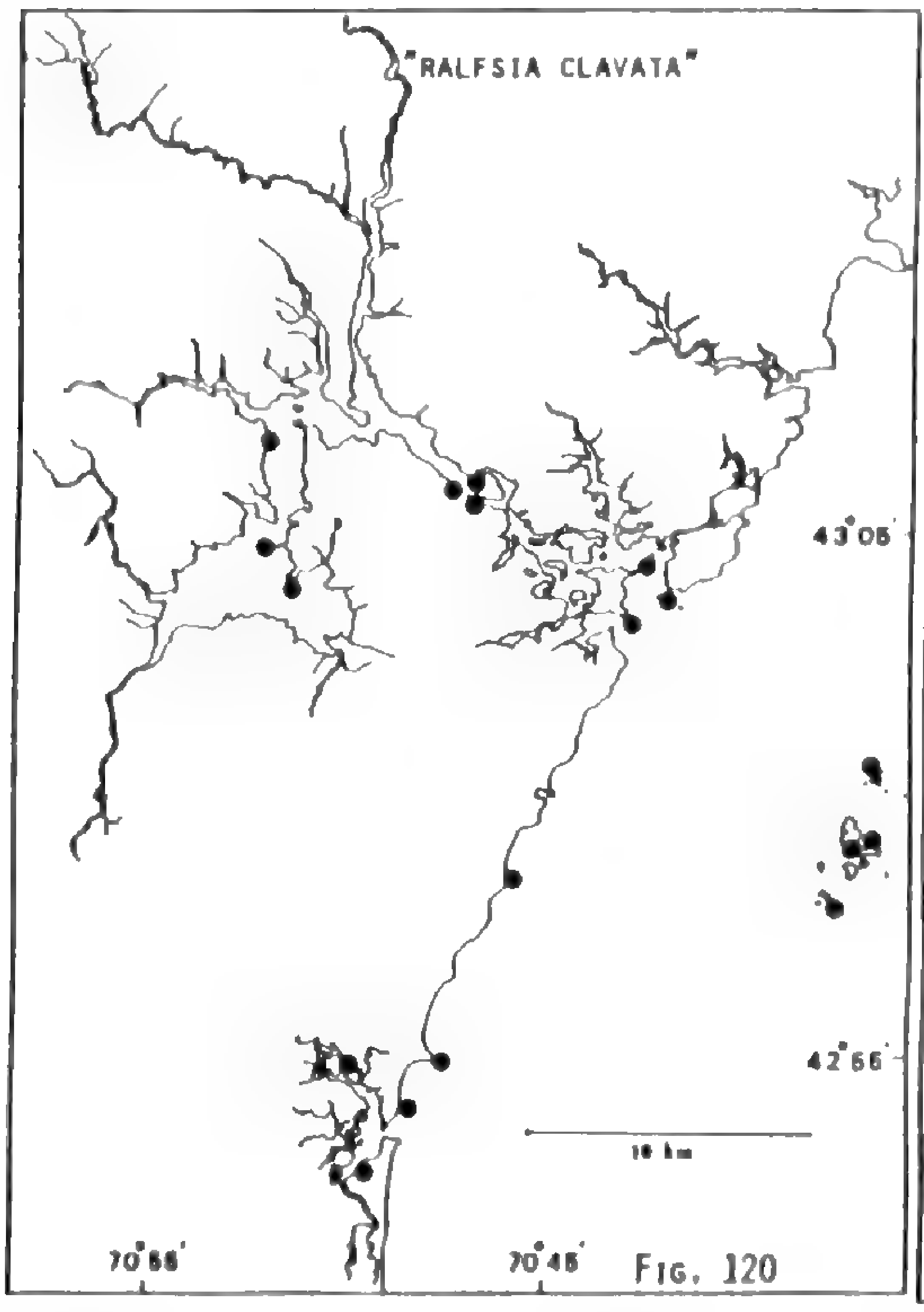


FIG. 120

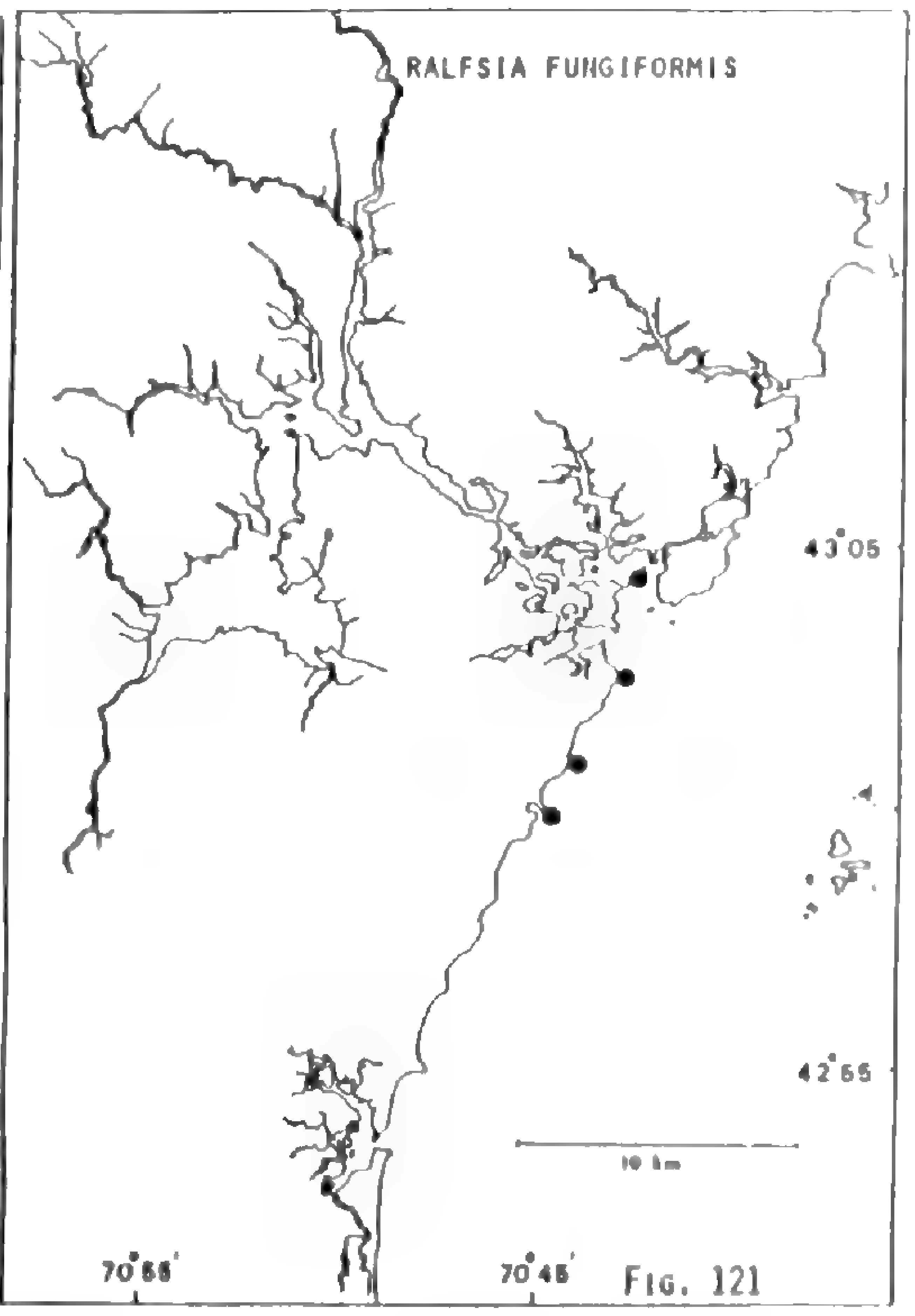


FIG. 121

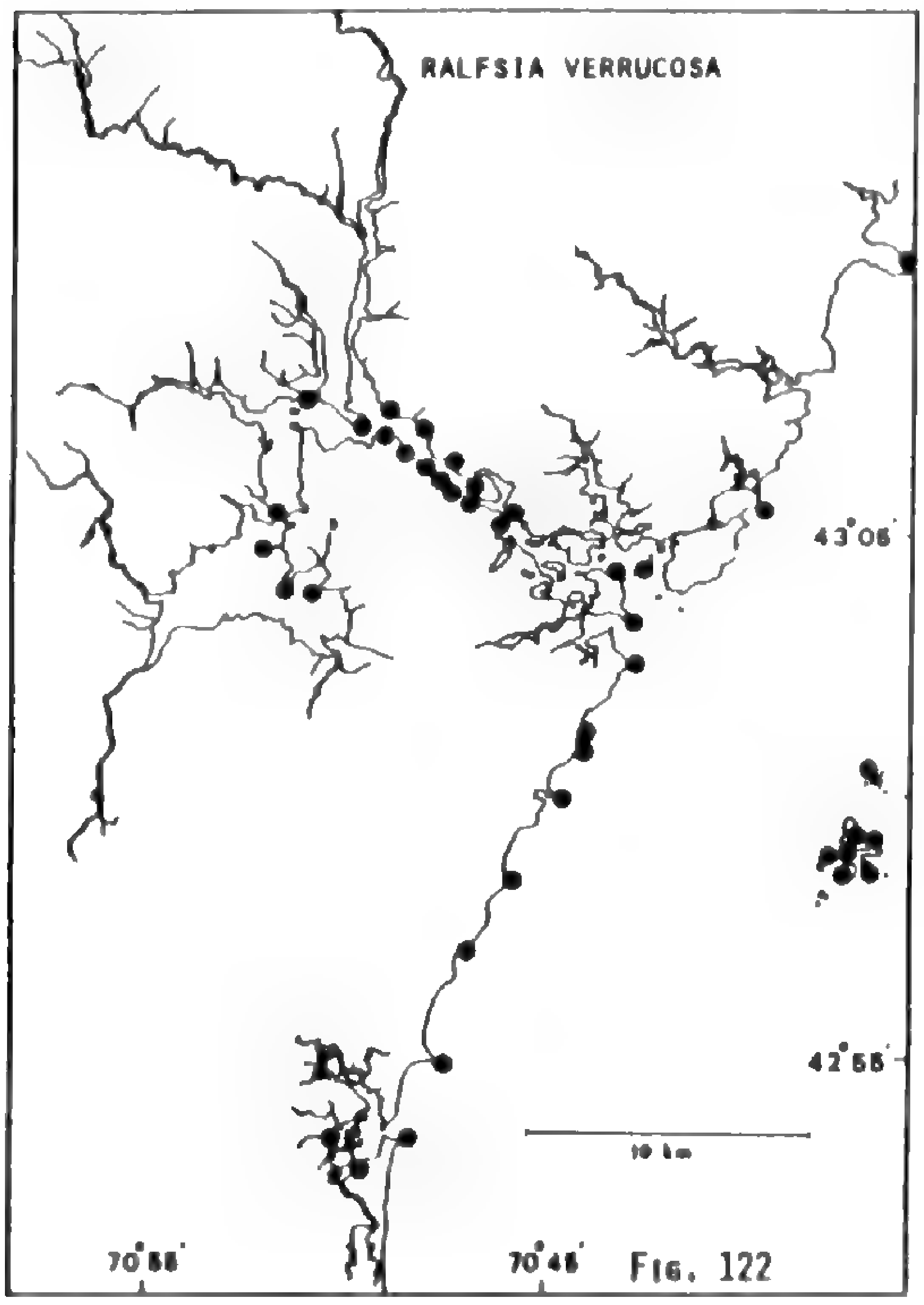


FIG. 122

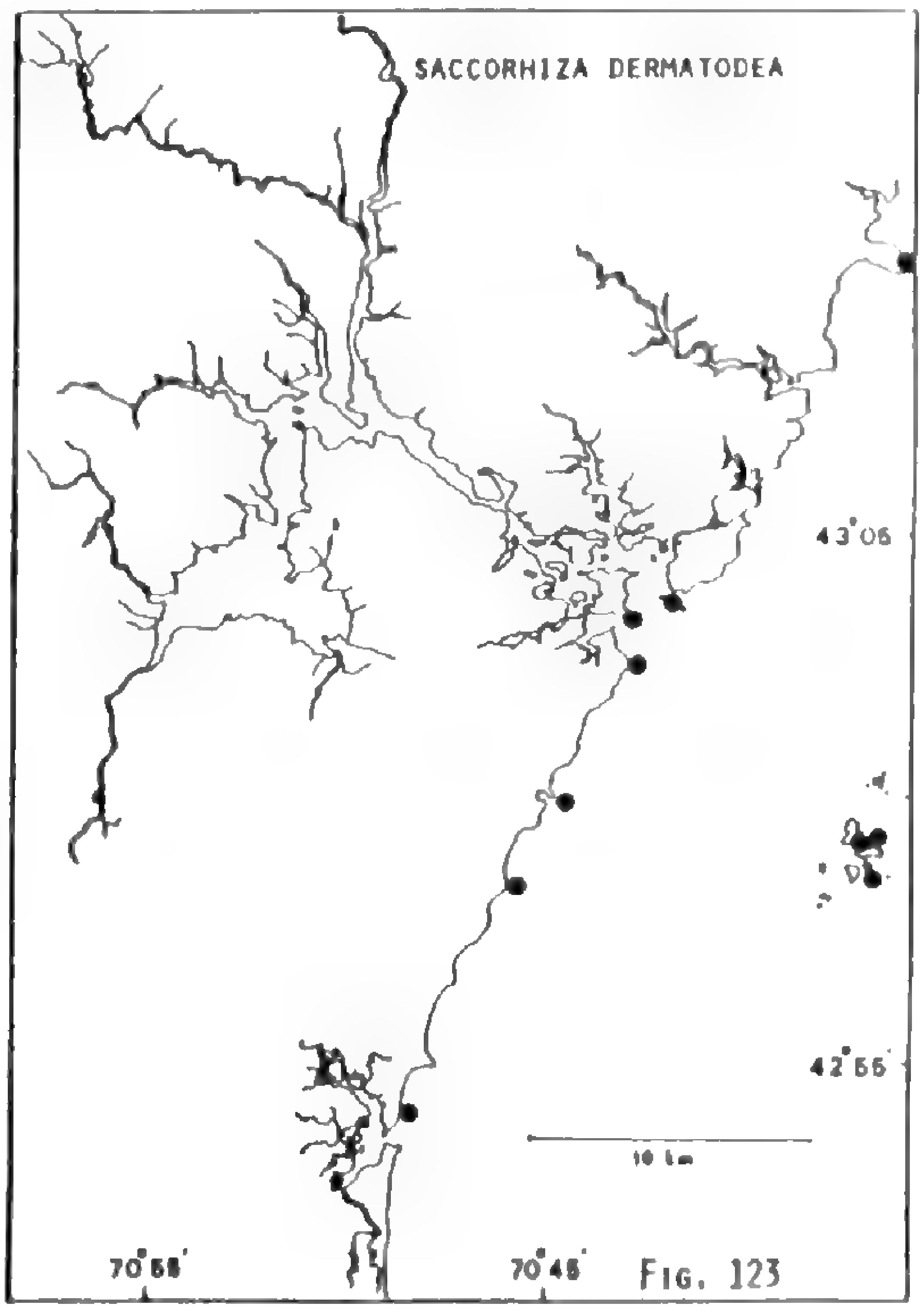


FIG. 123

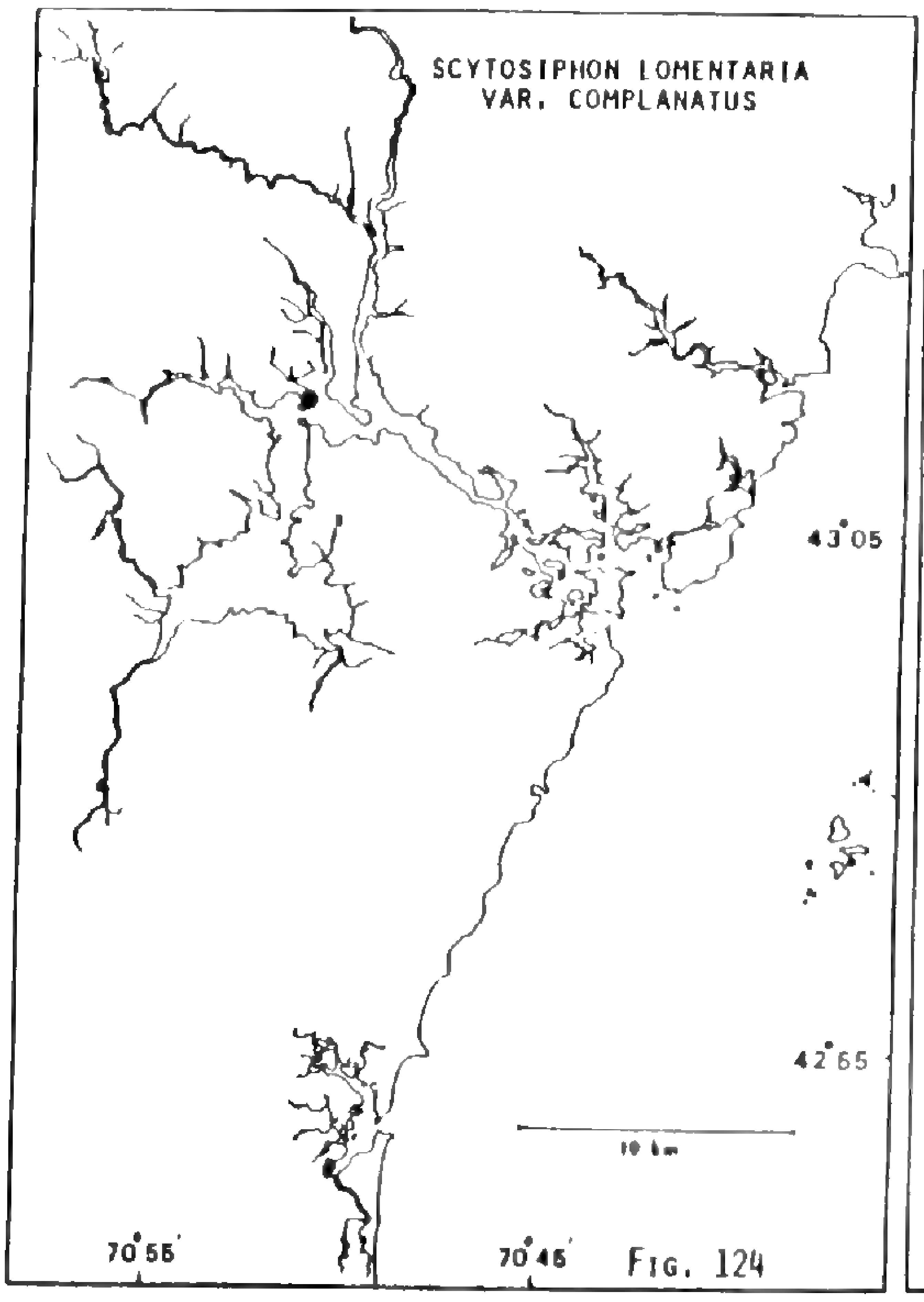


Fig. 124

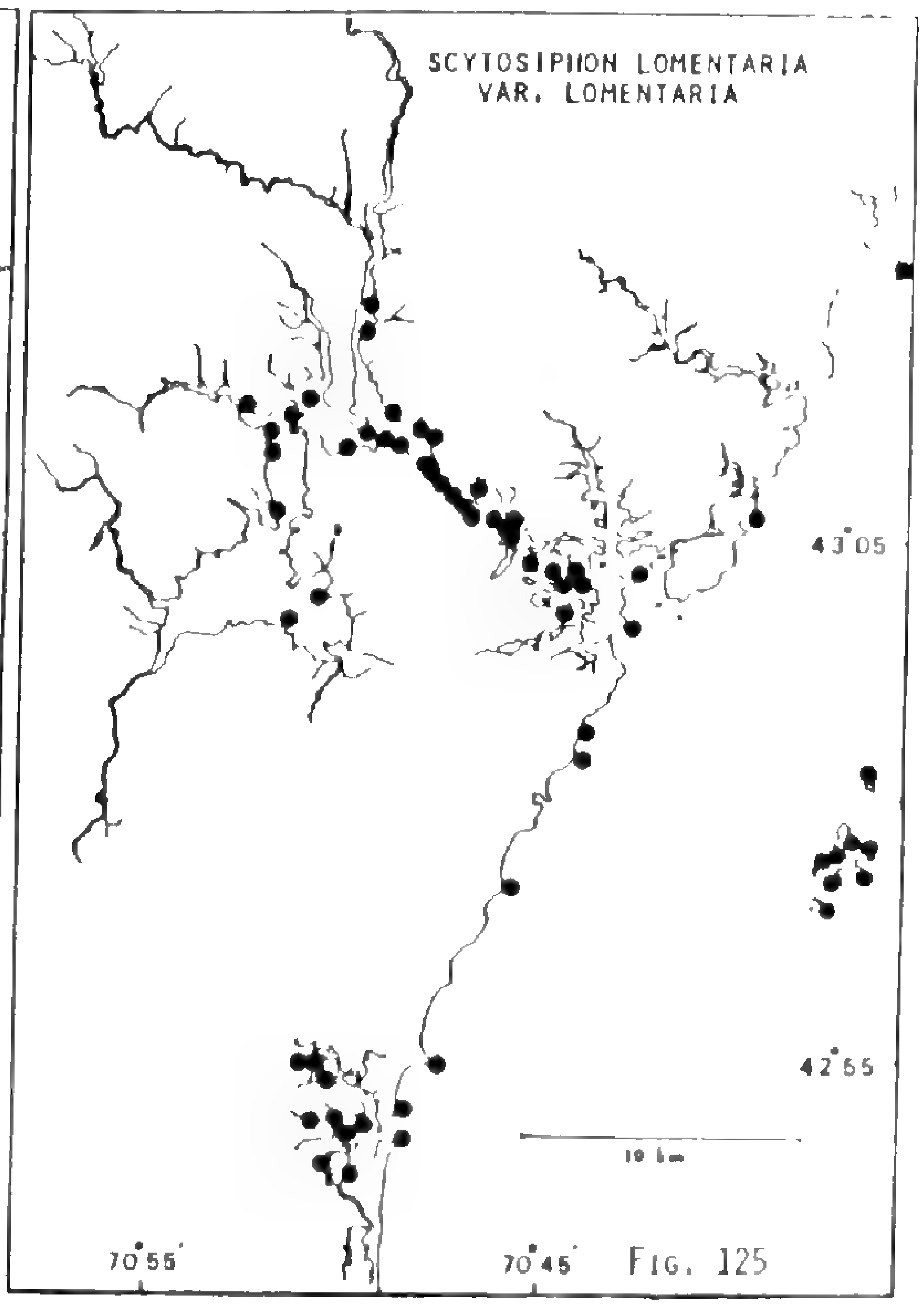


Fig. 125

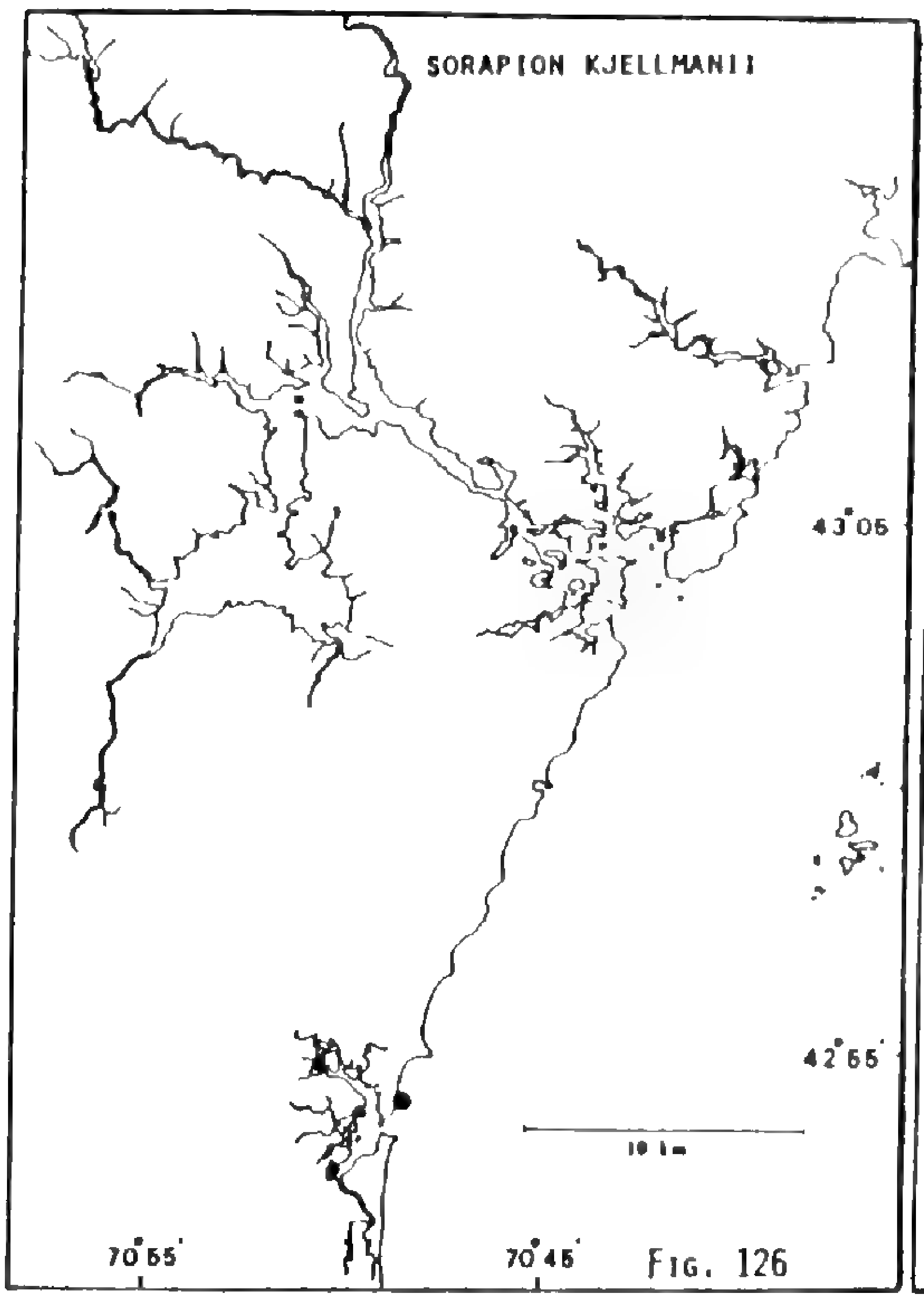


Fig. 126

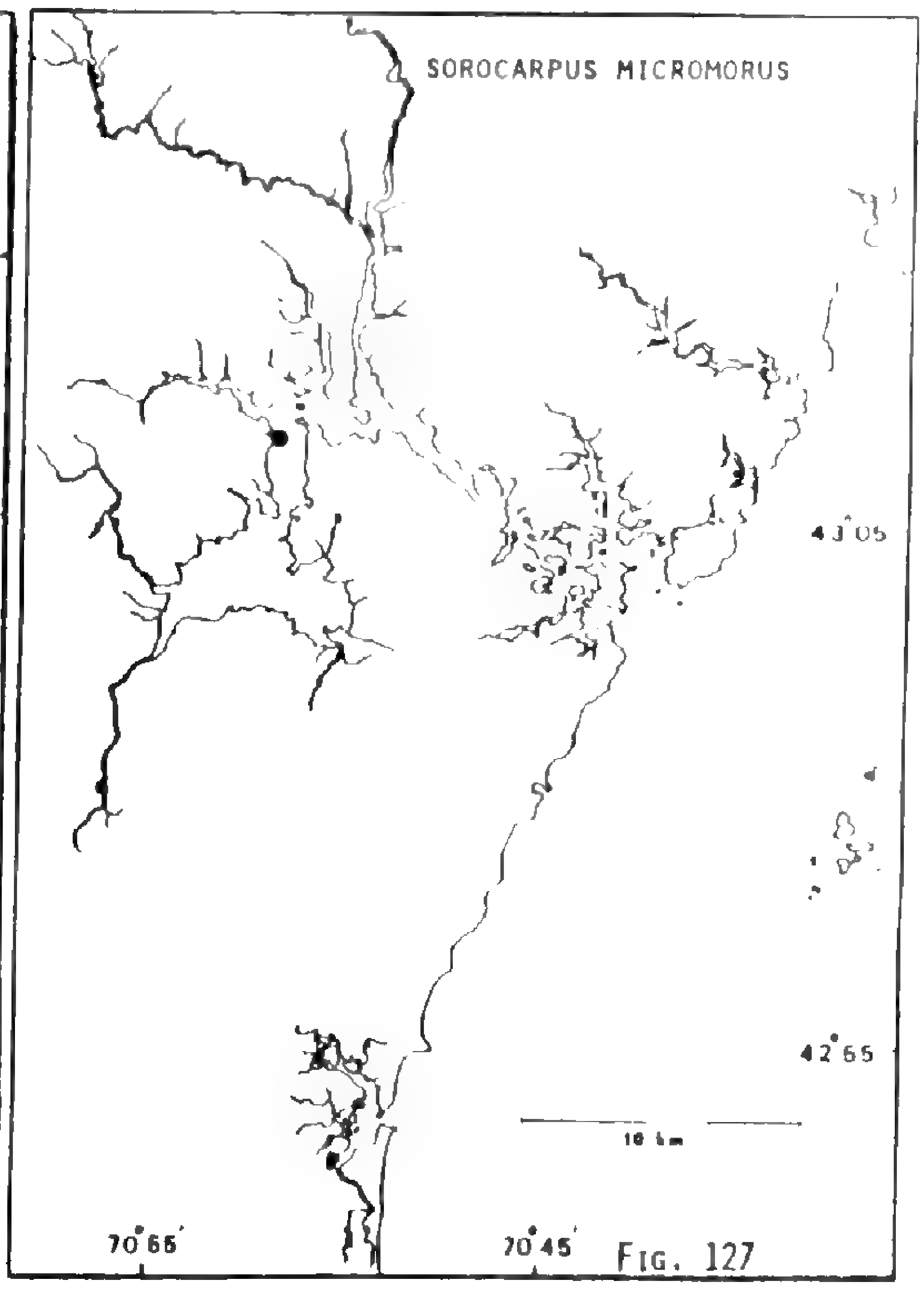


Fig. 127

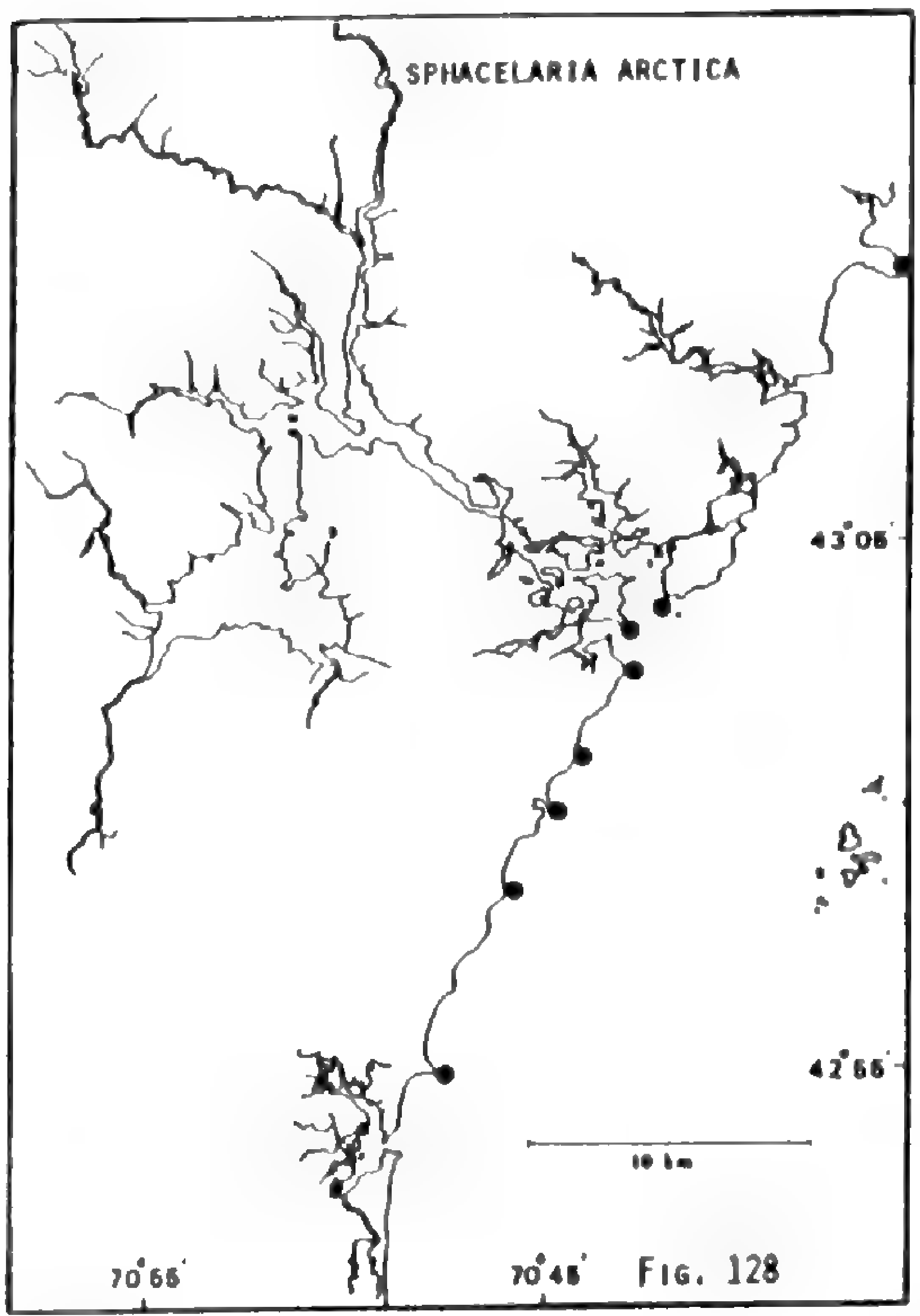


FIG. 128

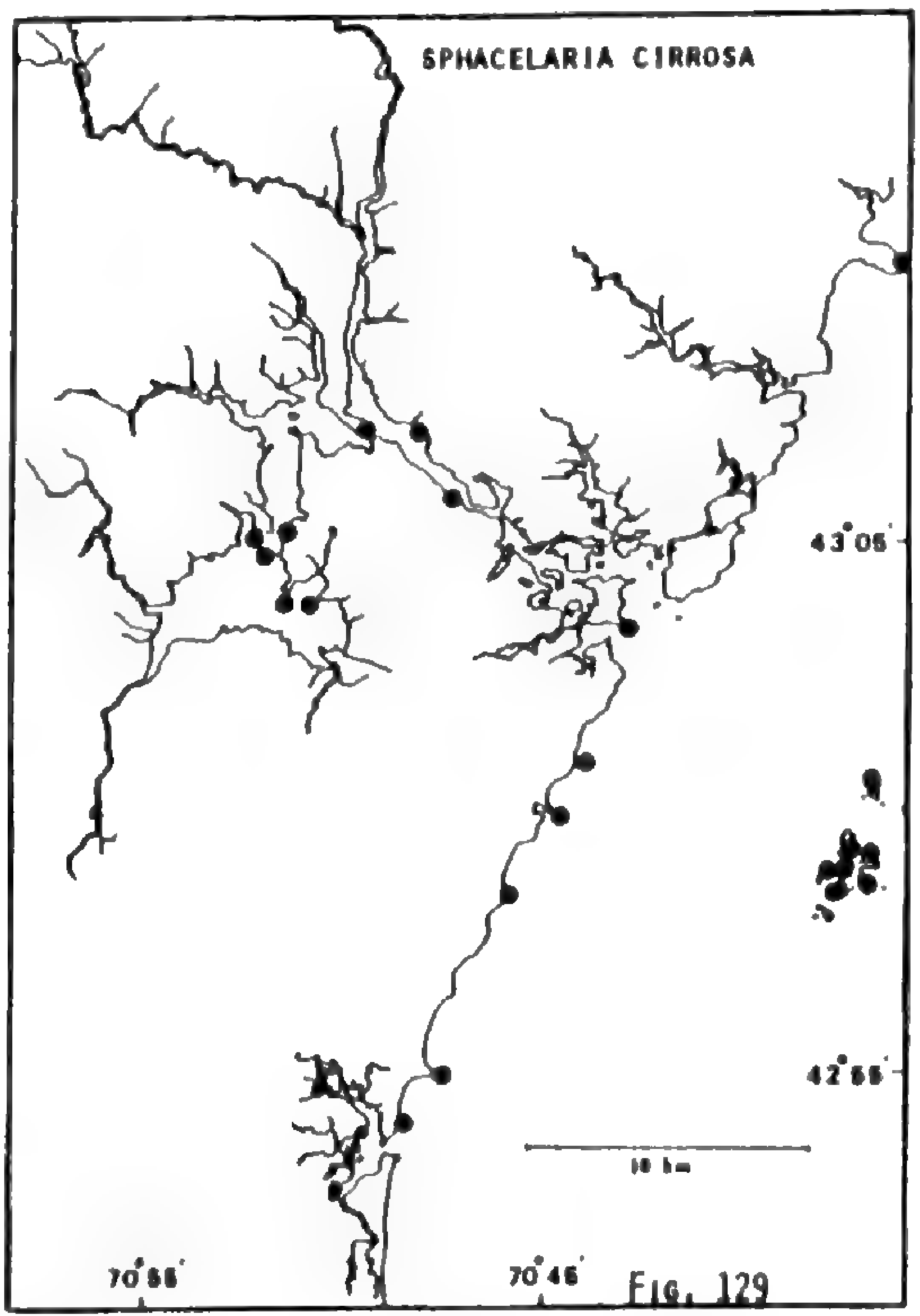


FIG. 129

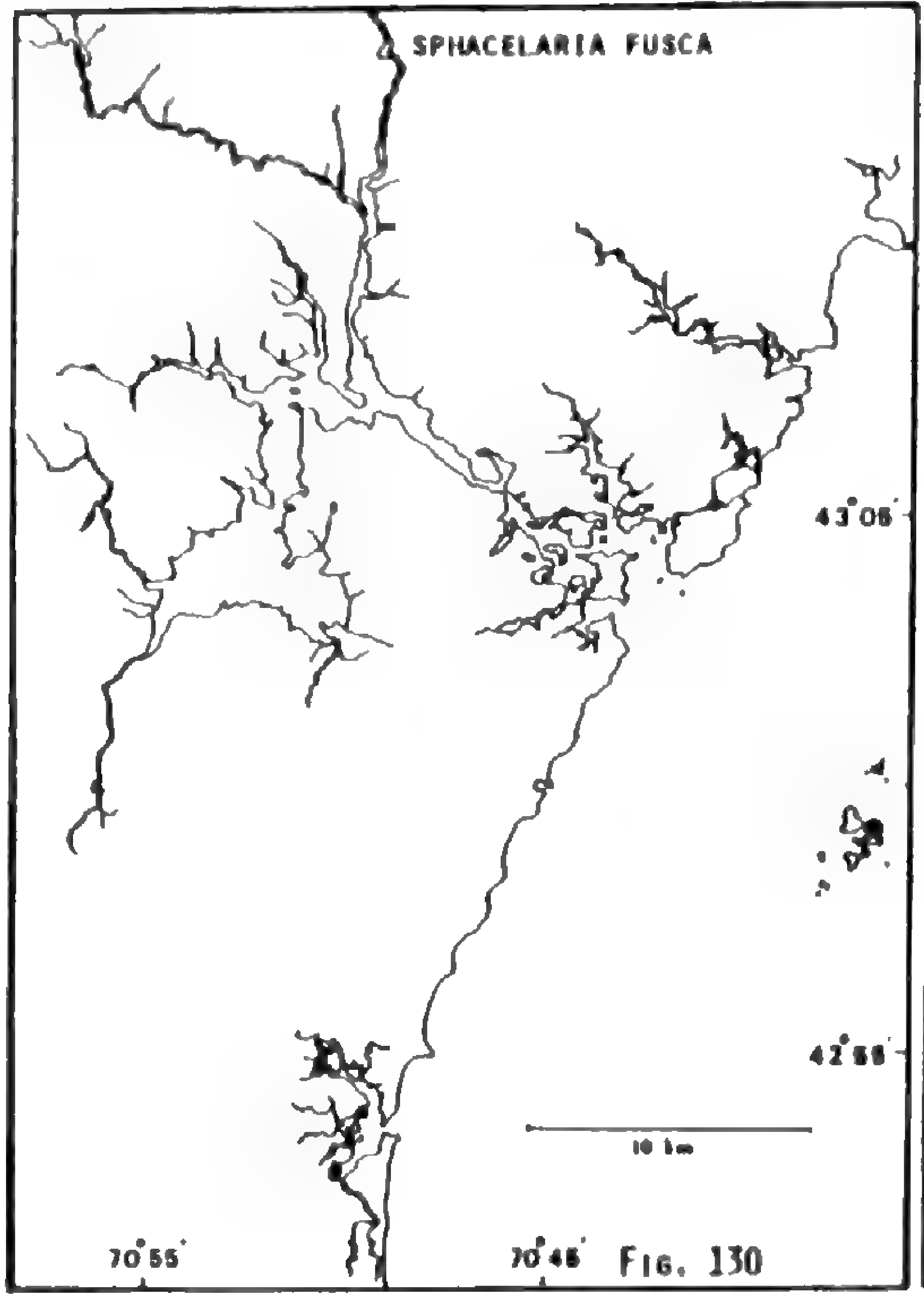


FIG. 130

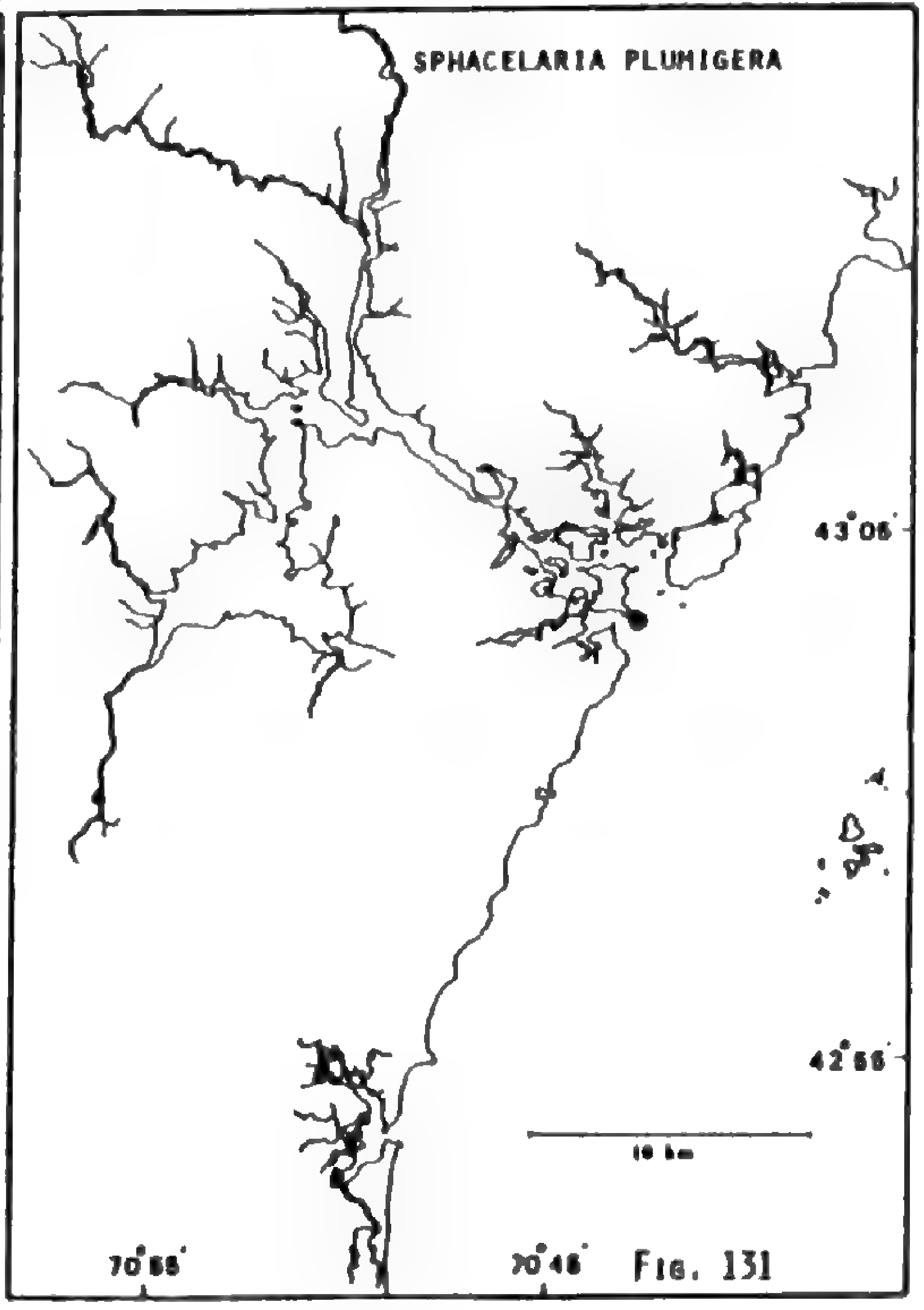


FIG. 131

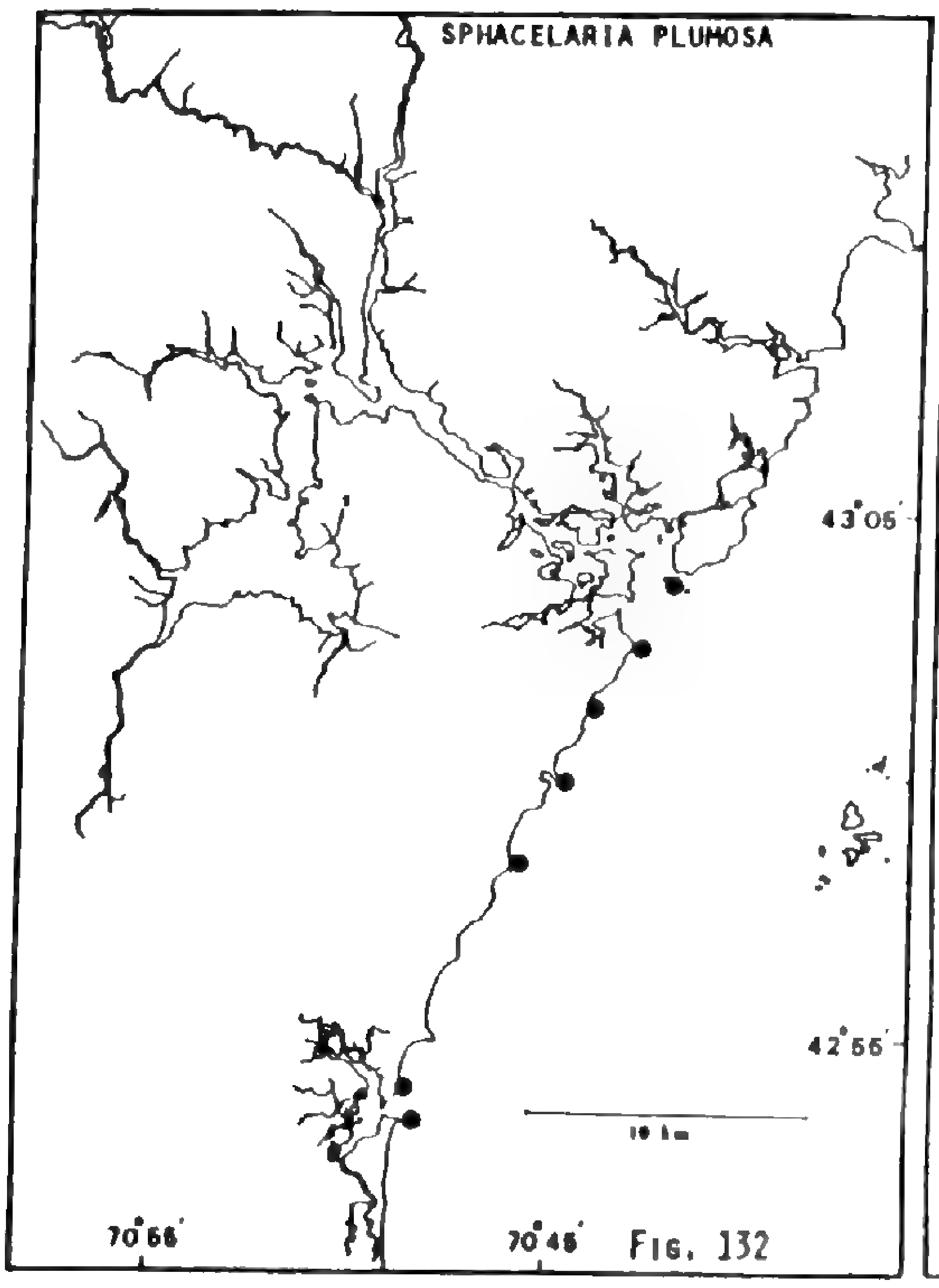


FIG. 132

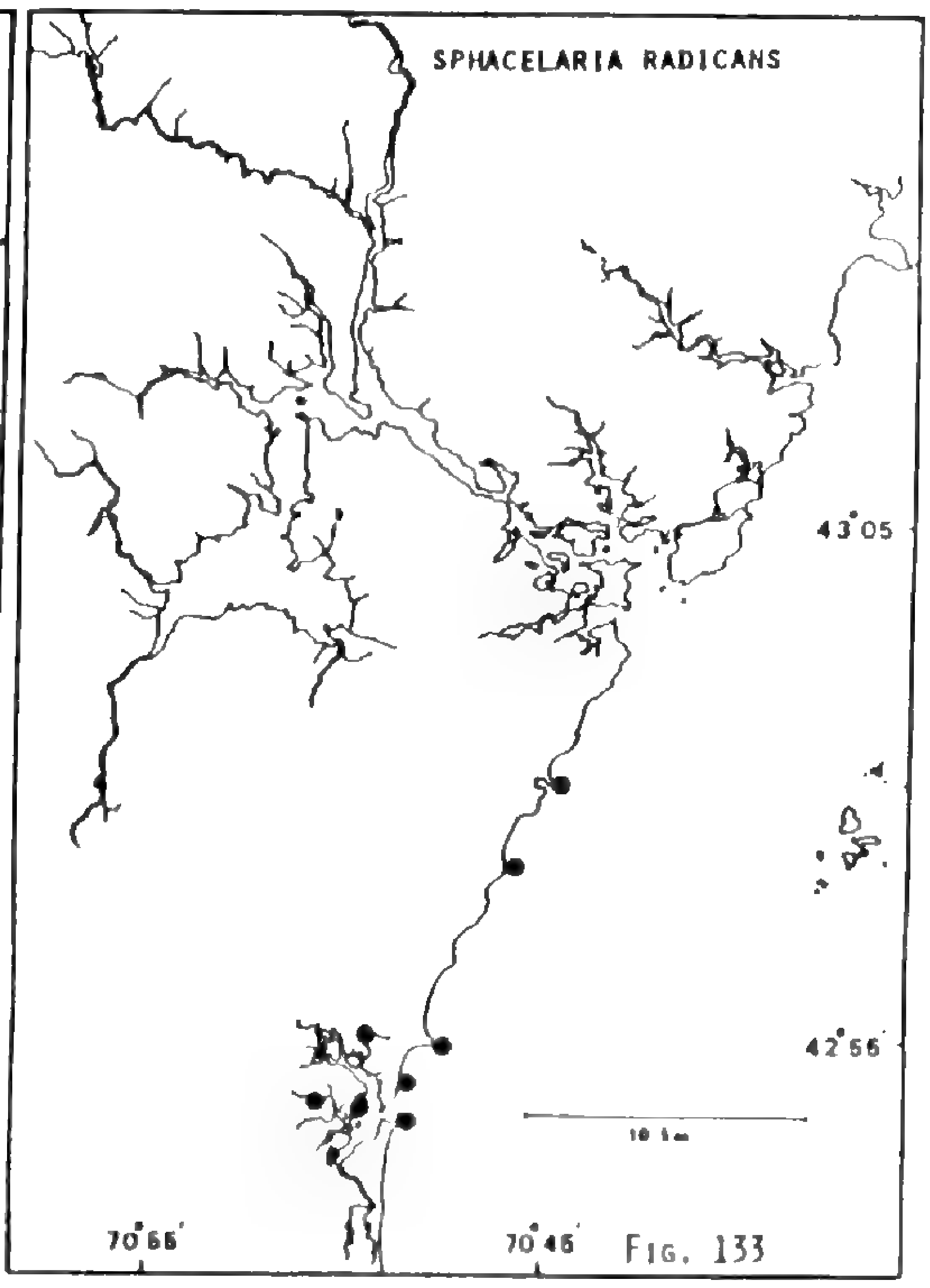


FIG. 133

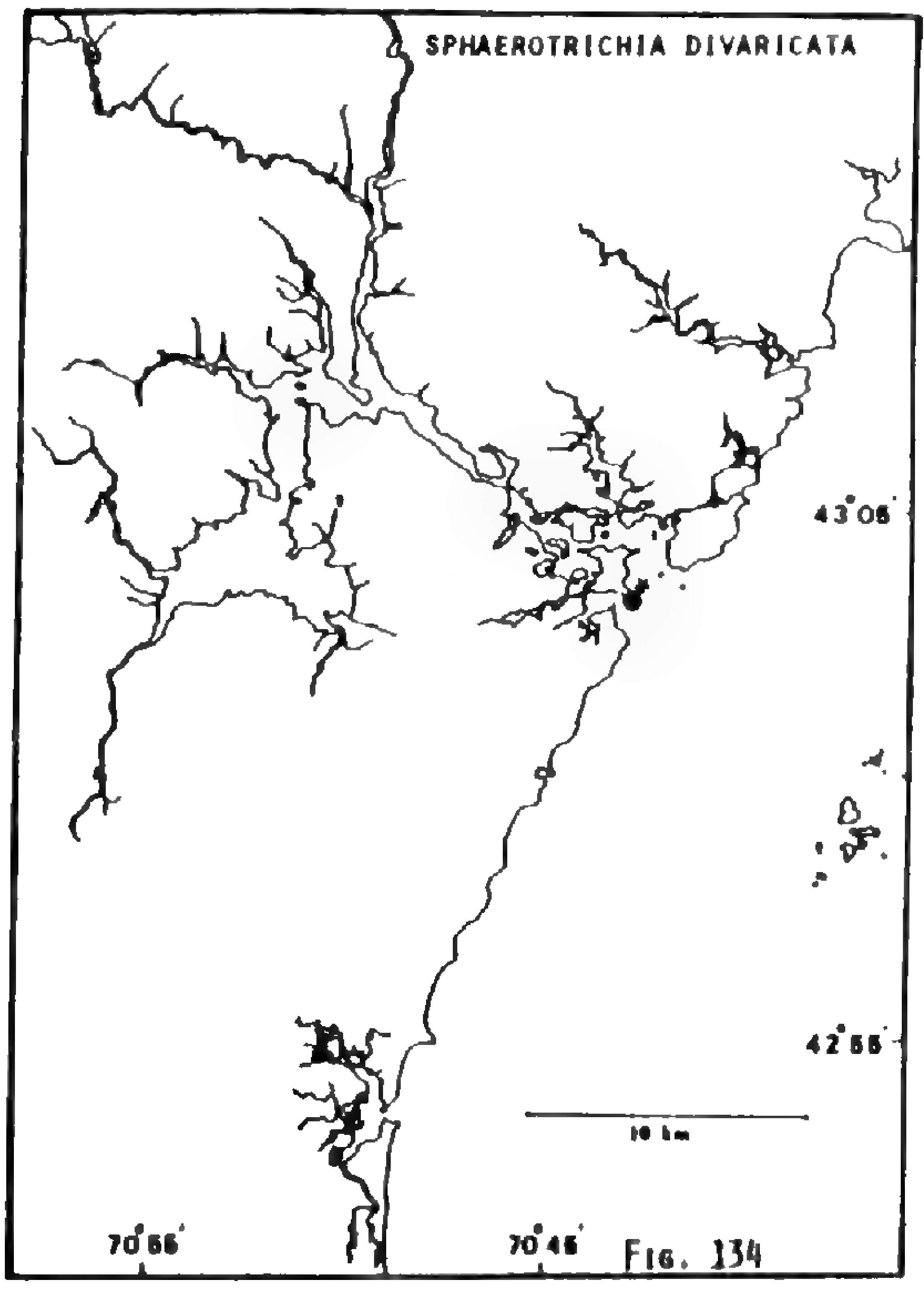


FIG. 134

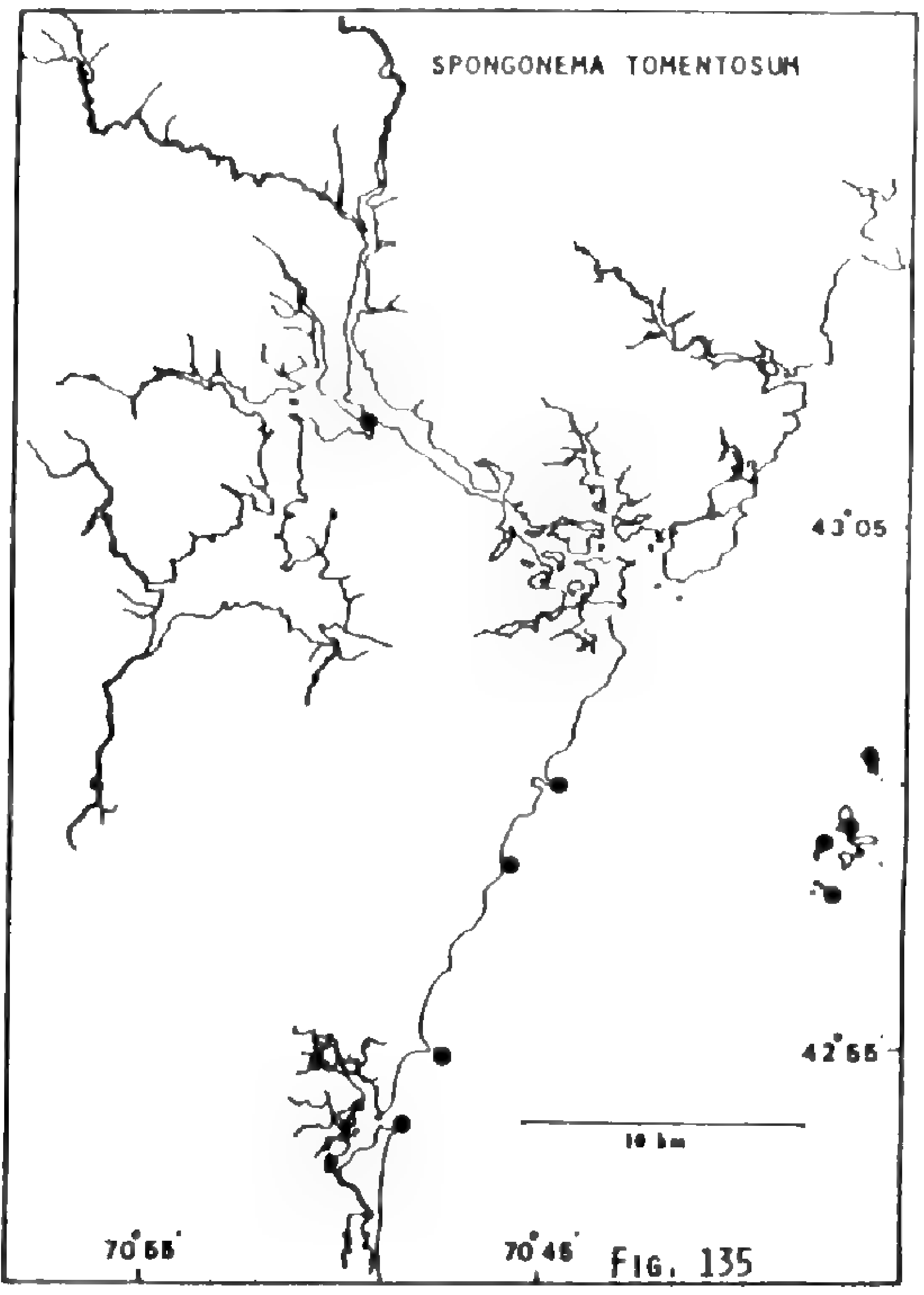


FIG. 135

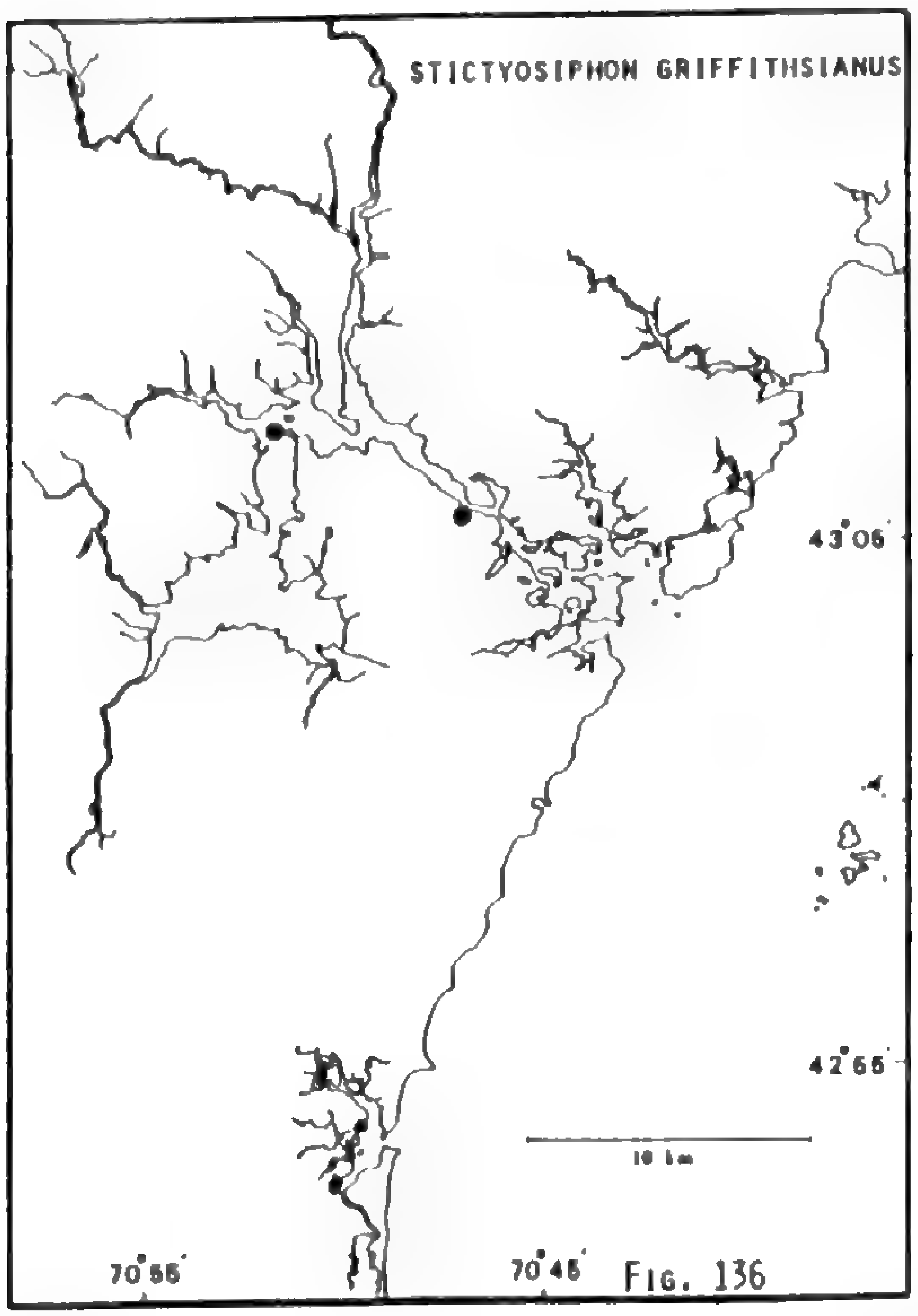


FIG. 136

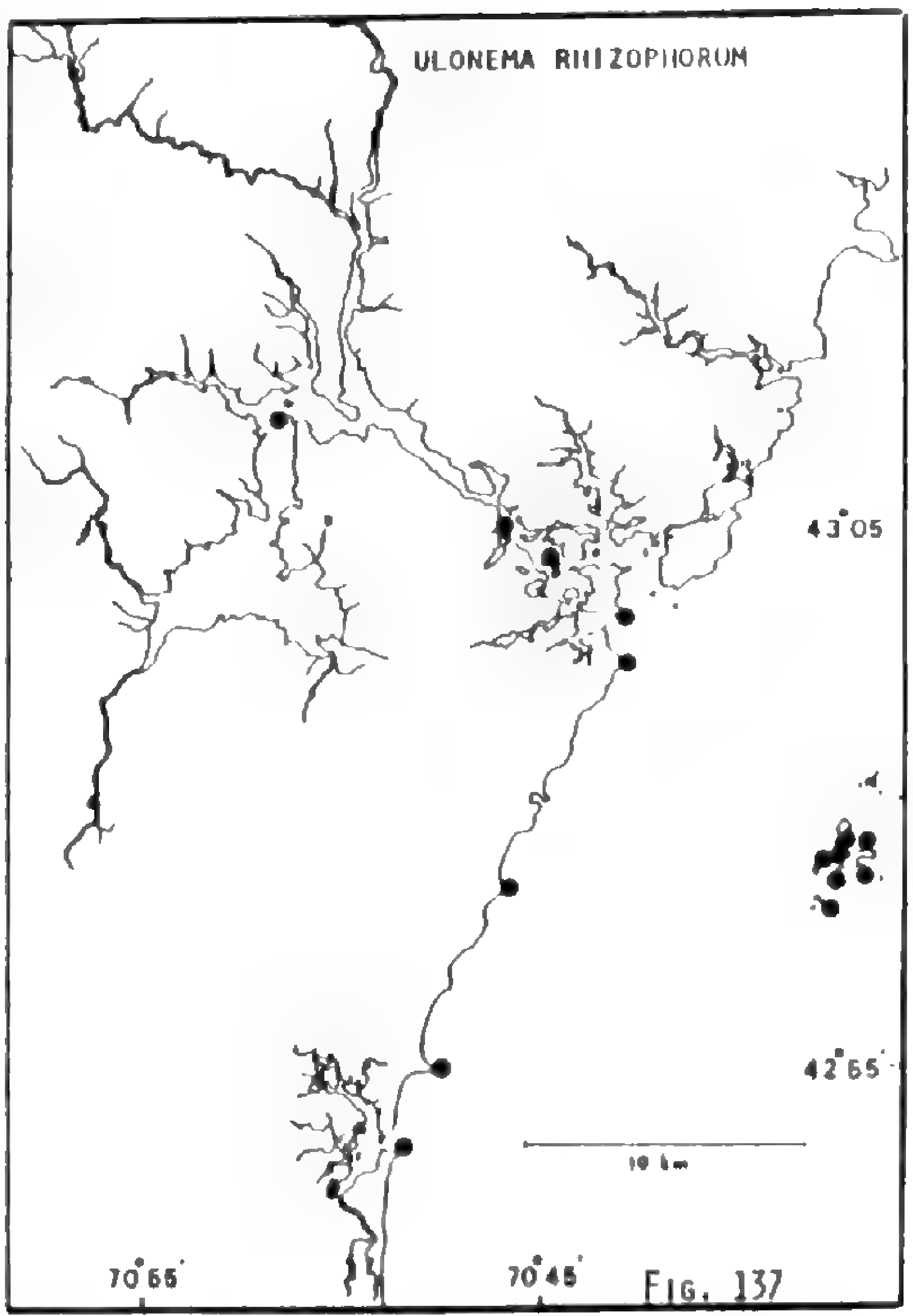


FIG. 137

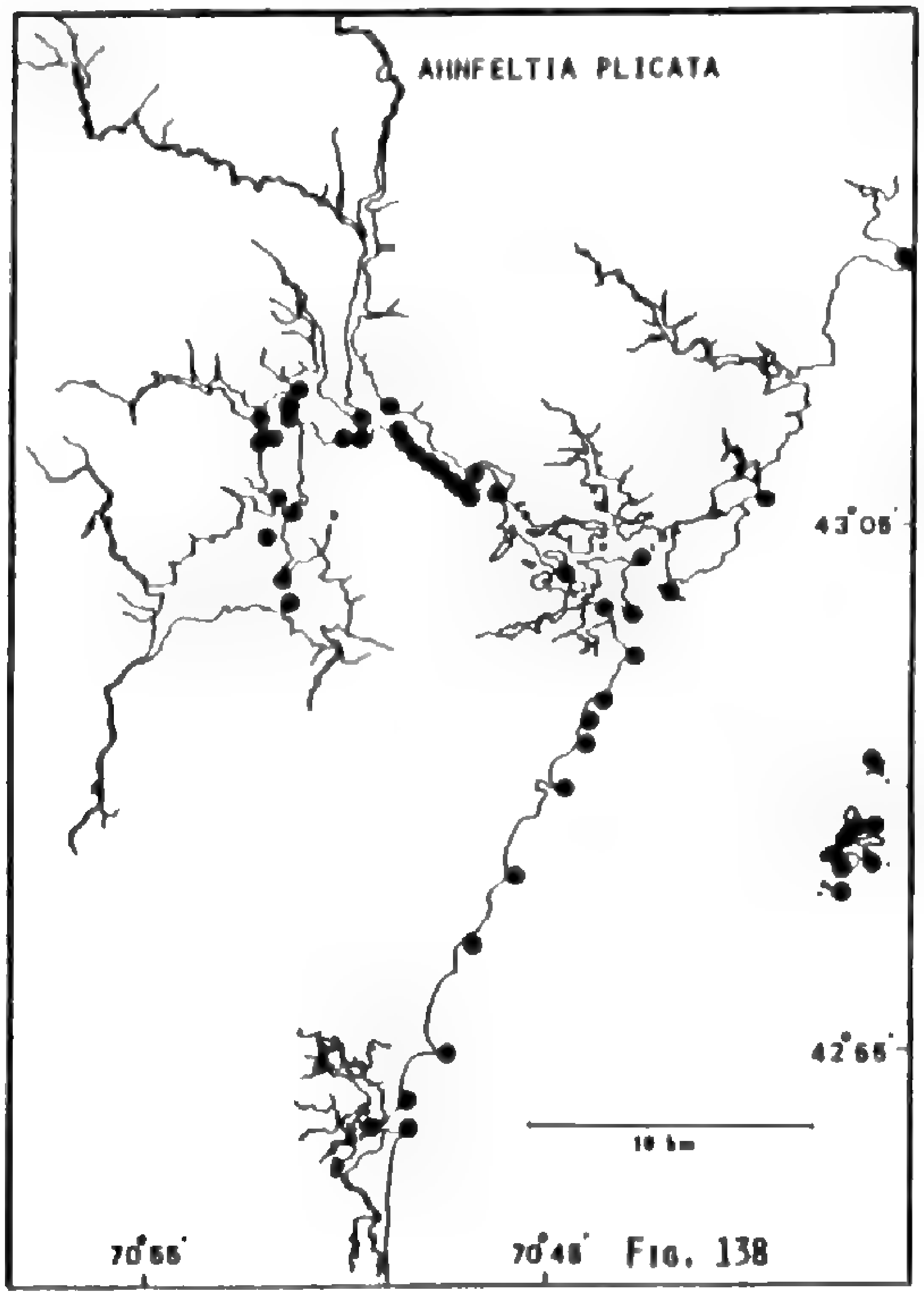


FIG. 138

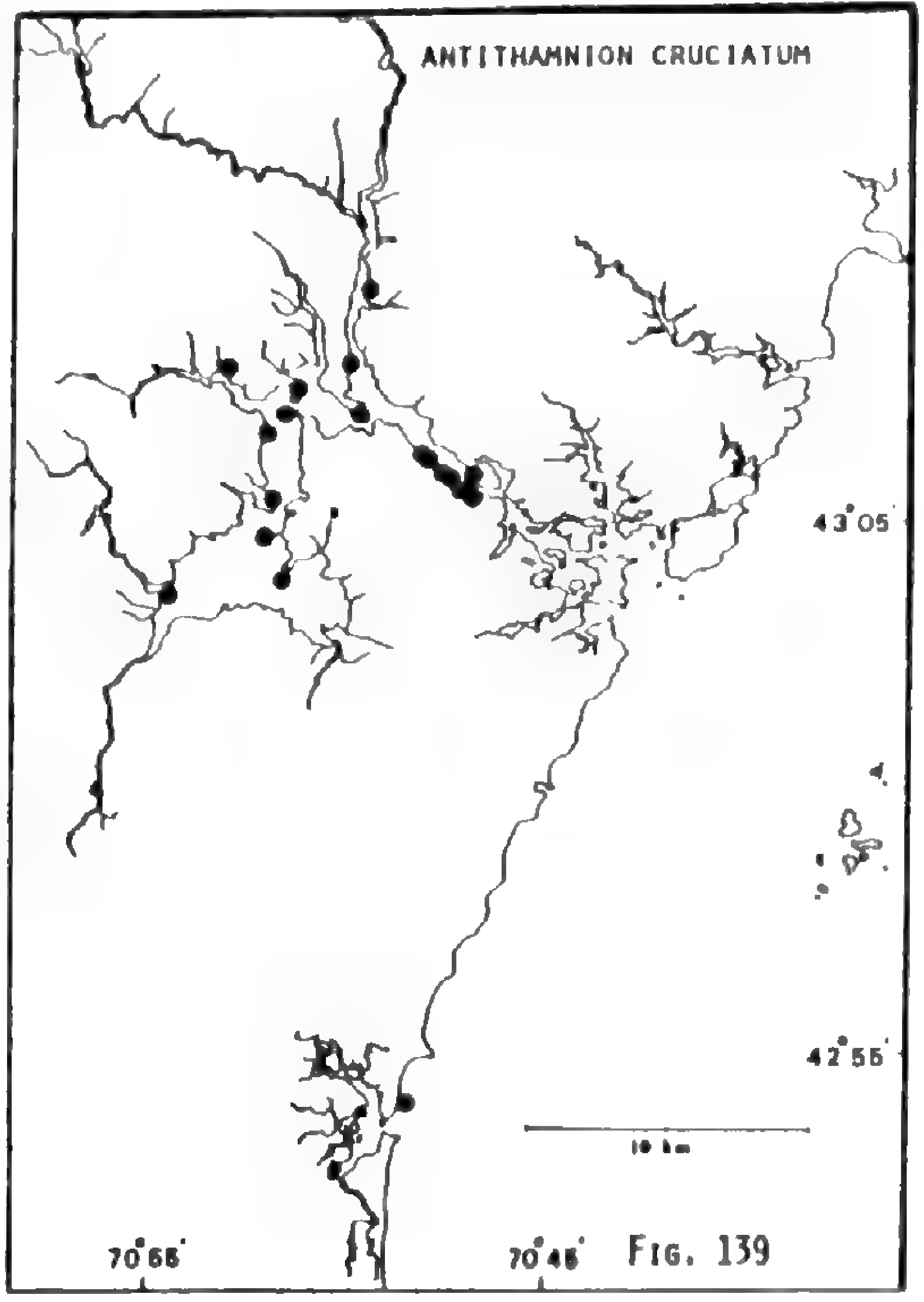


FIG. 139

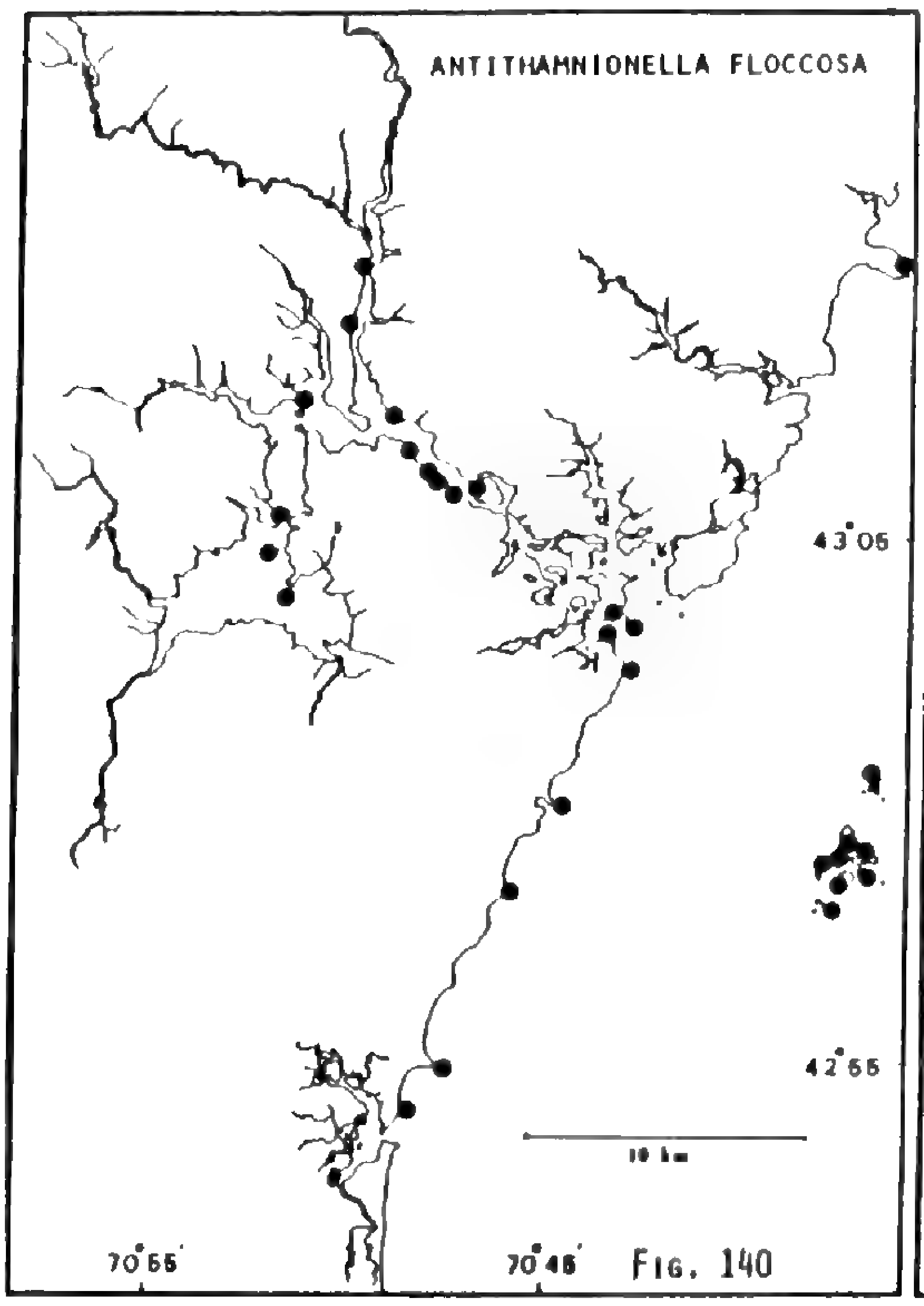


FIG. 140

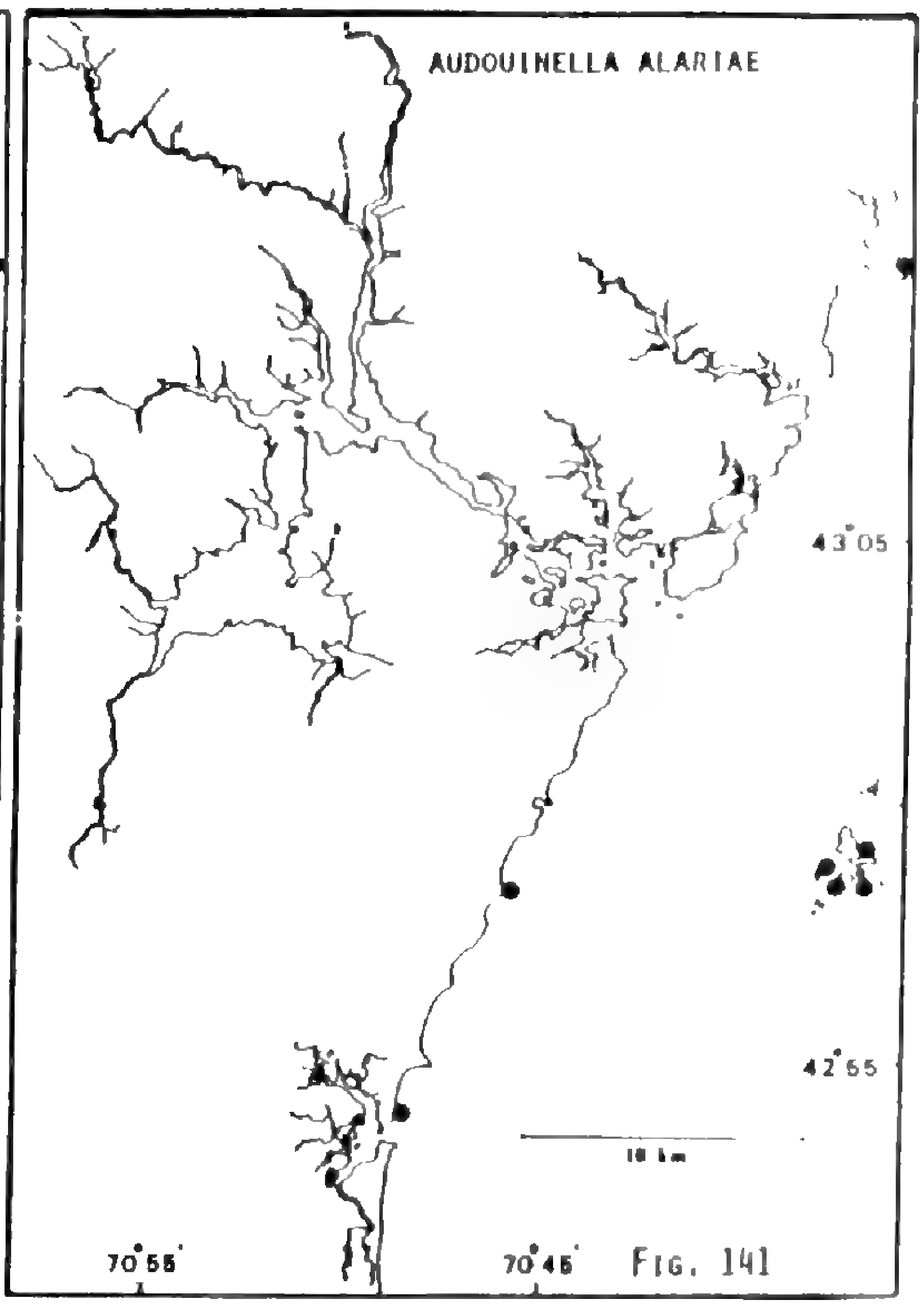


FIG. 141

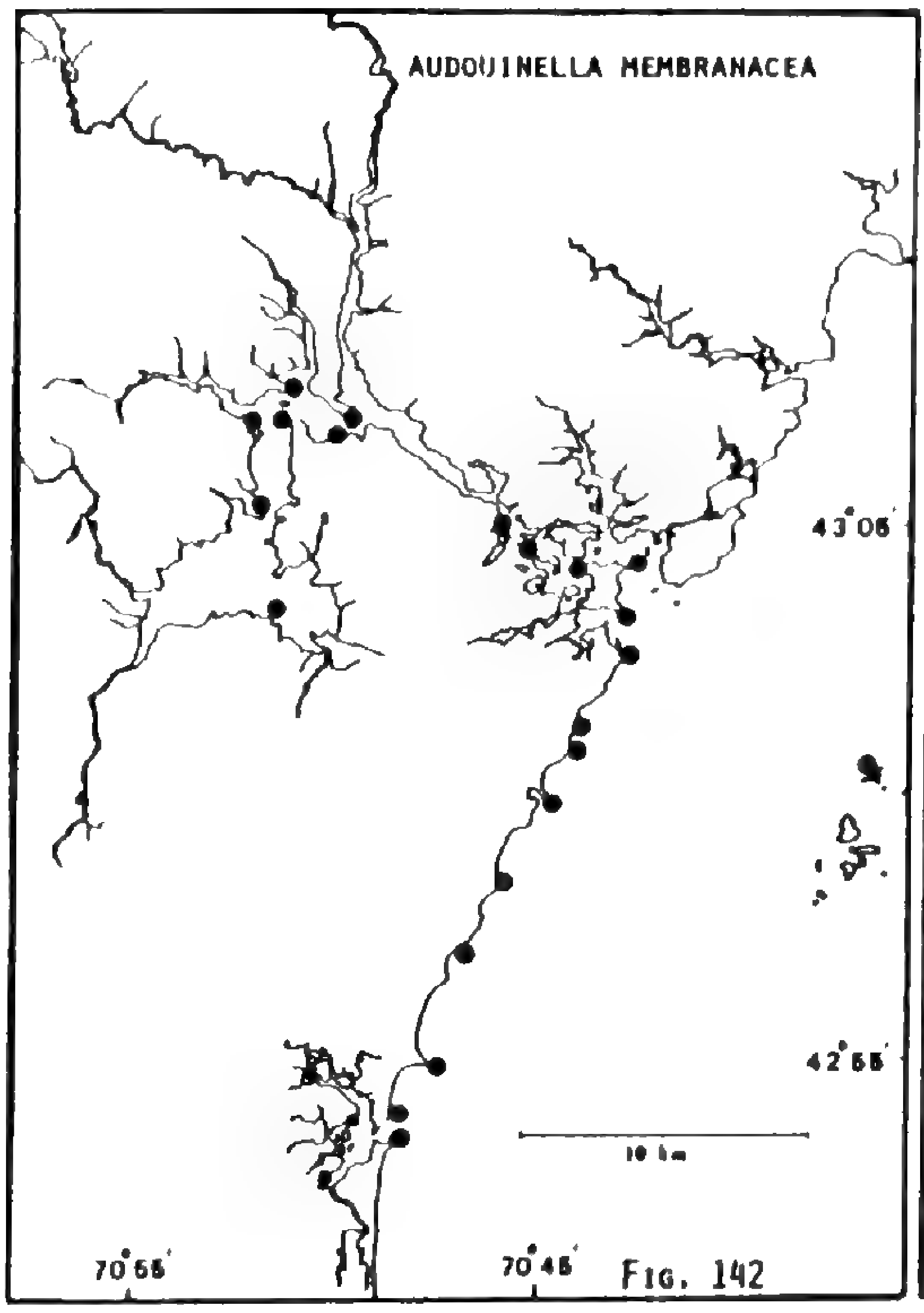


FIG. 142

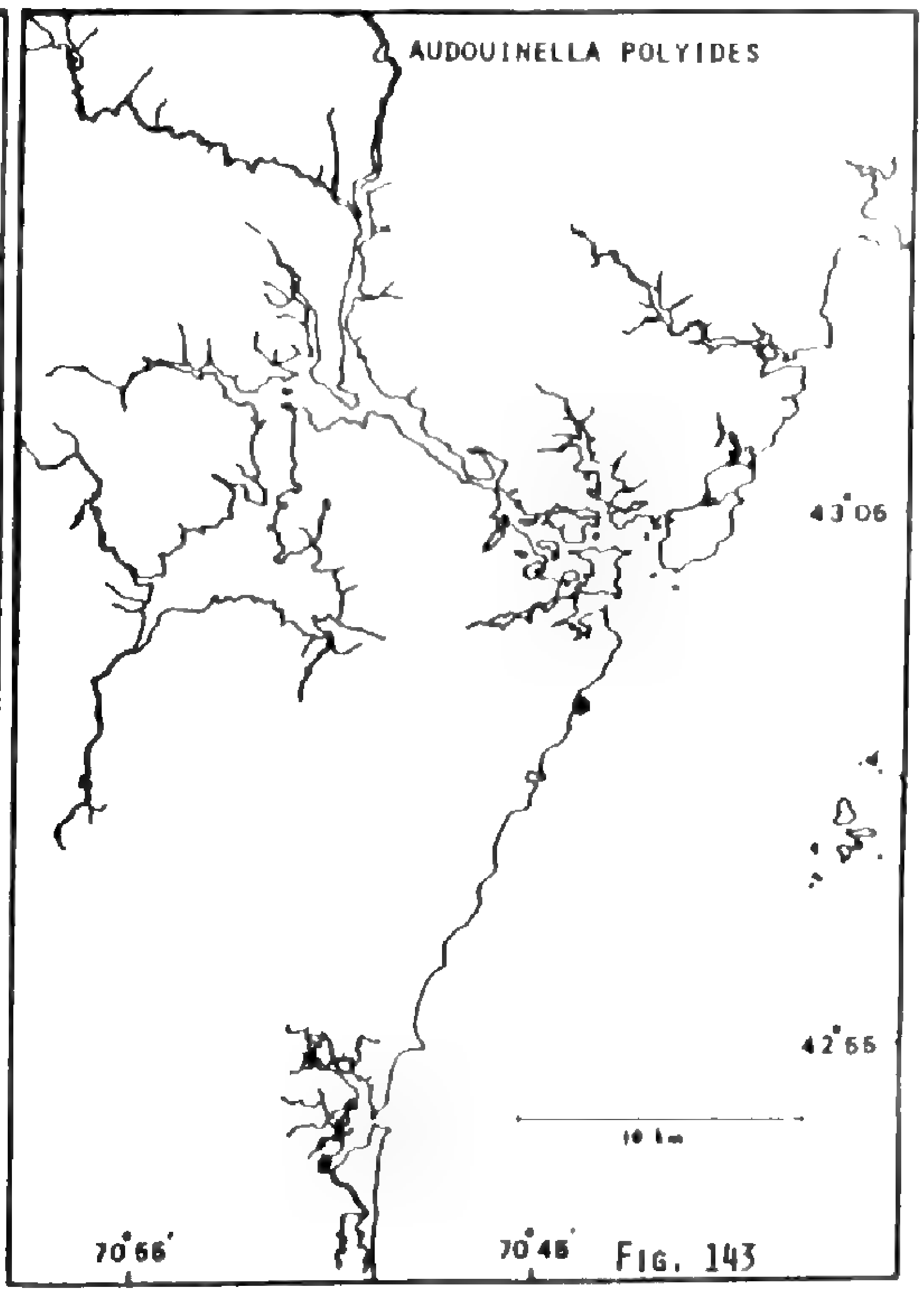


FIG. 143

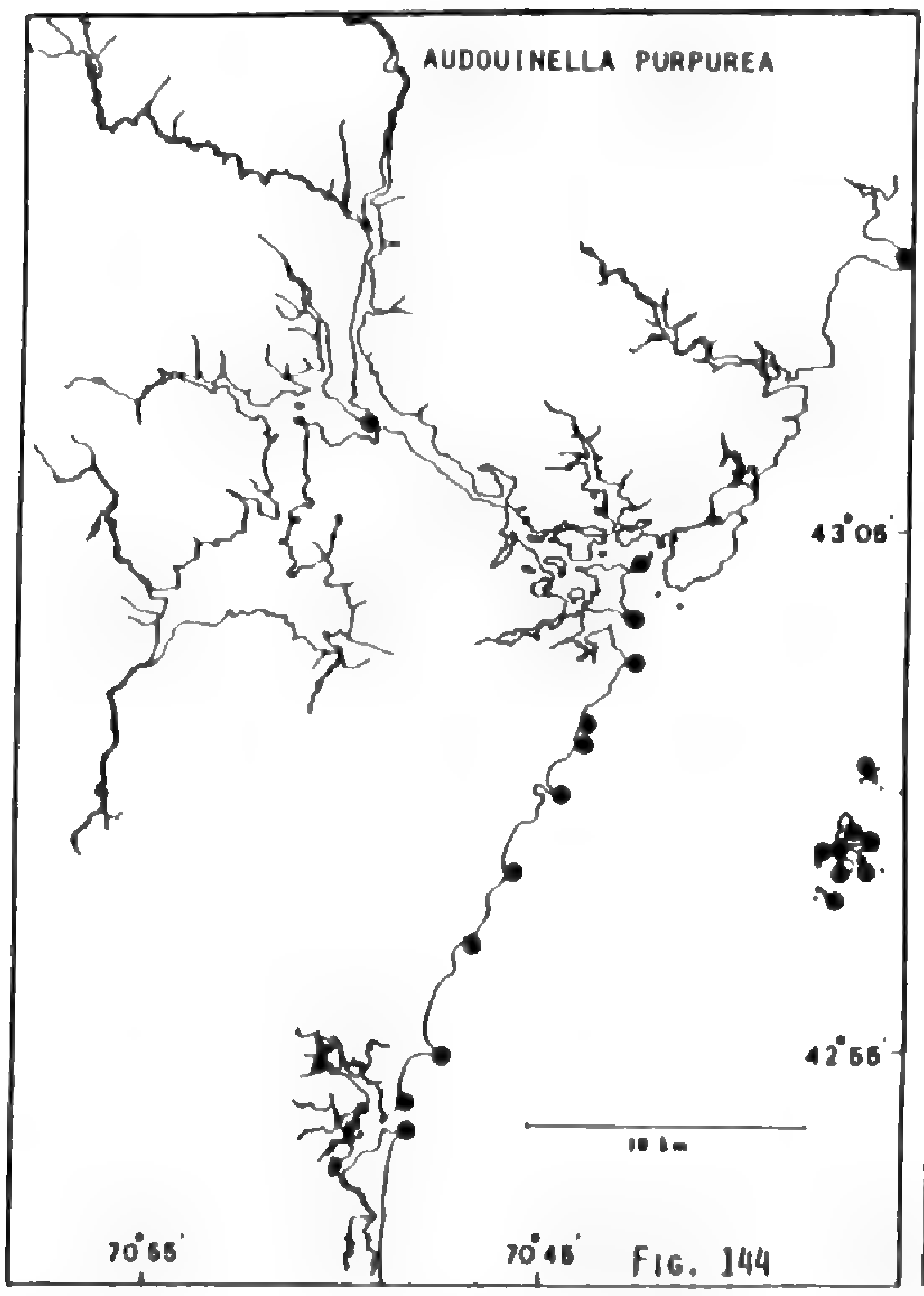


Fig. 144

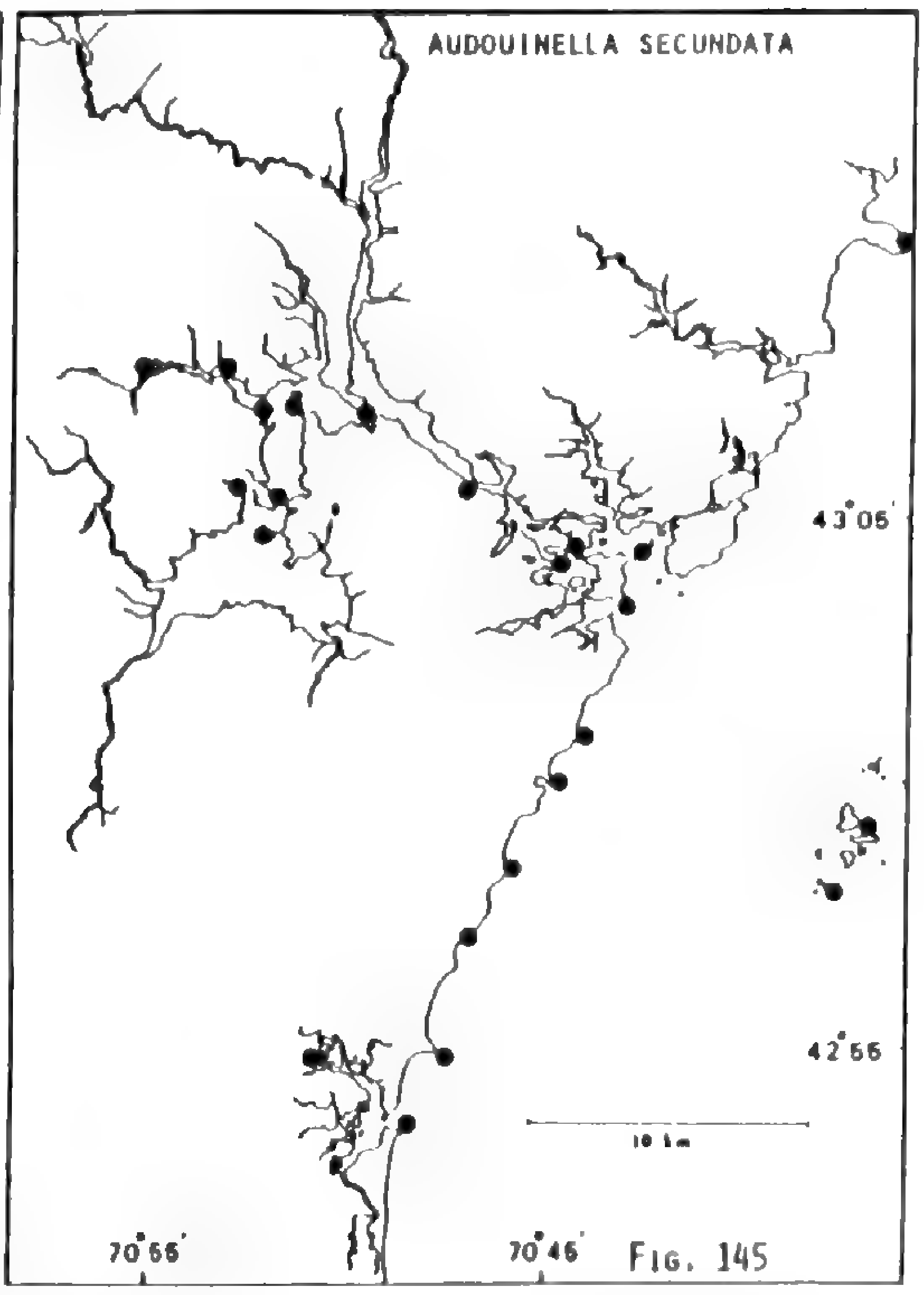


Fig. 145

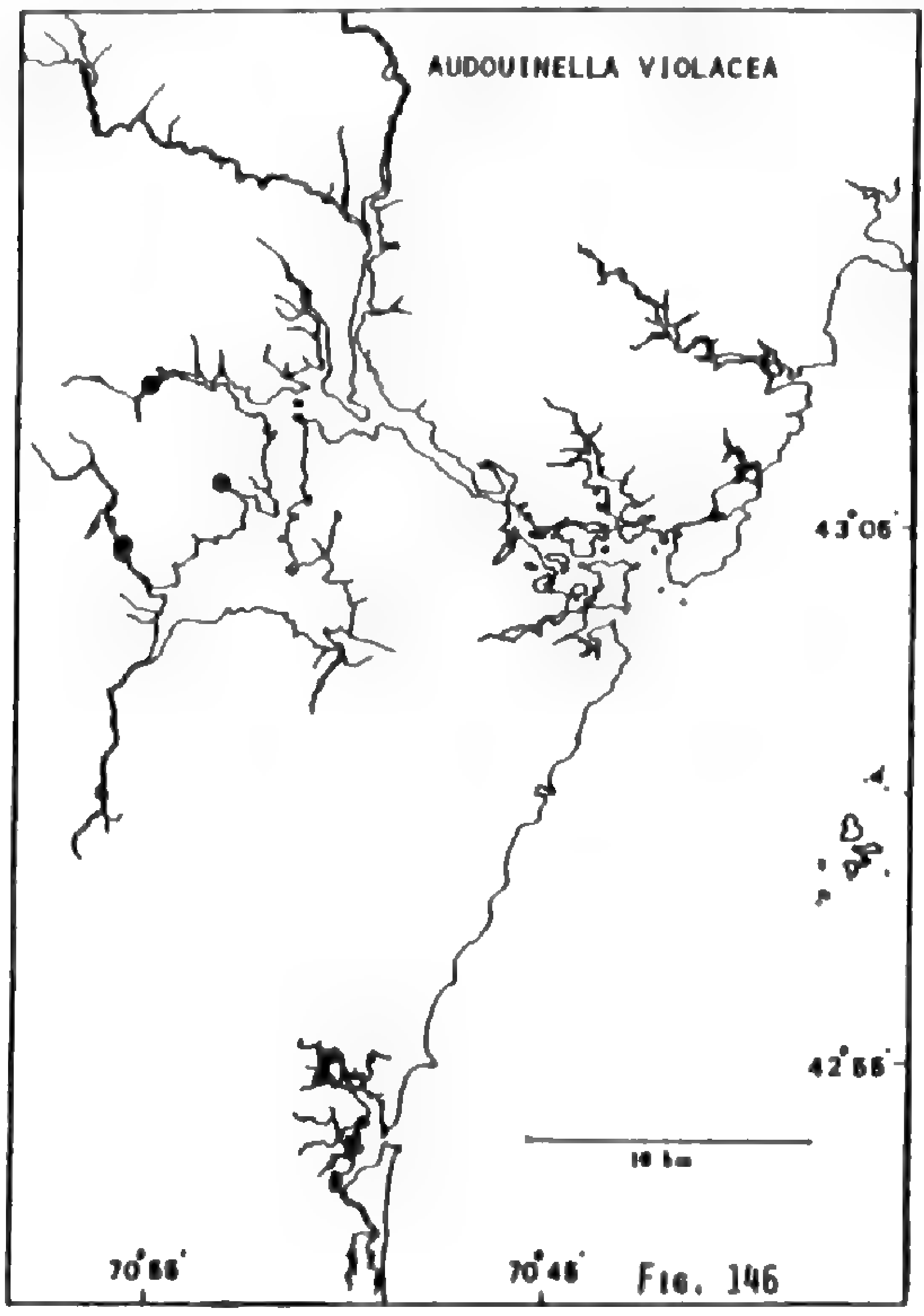


Fig. 146

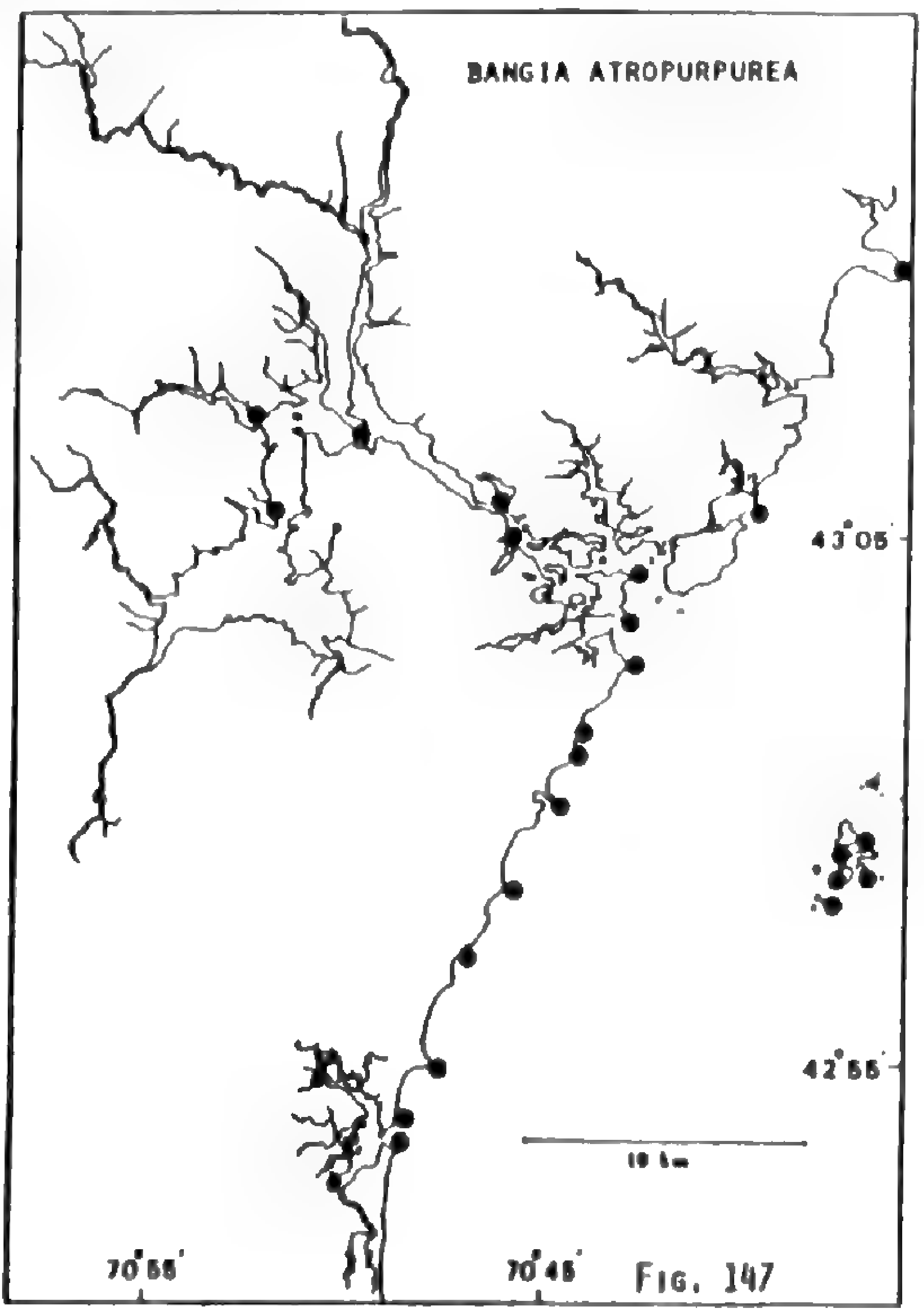


Fig. 147

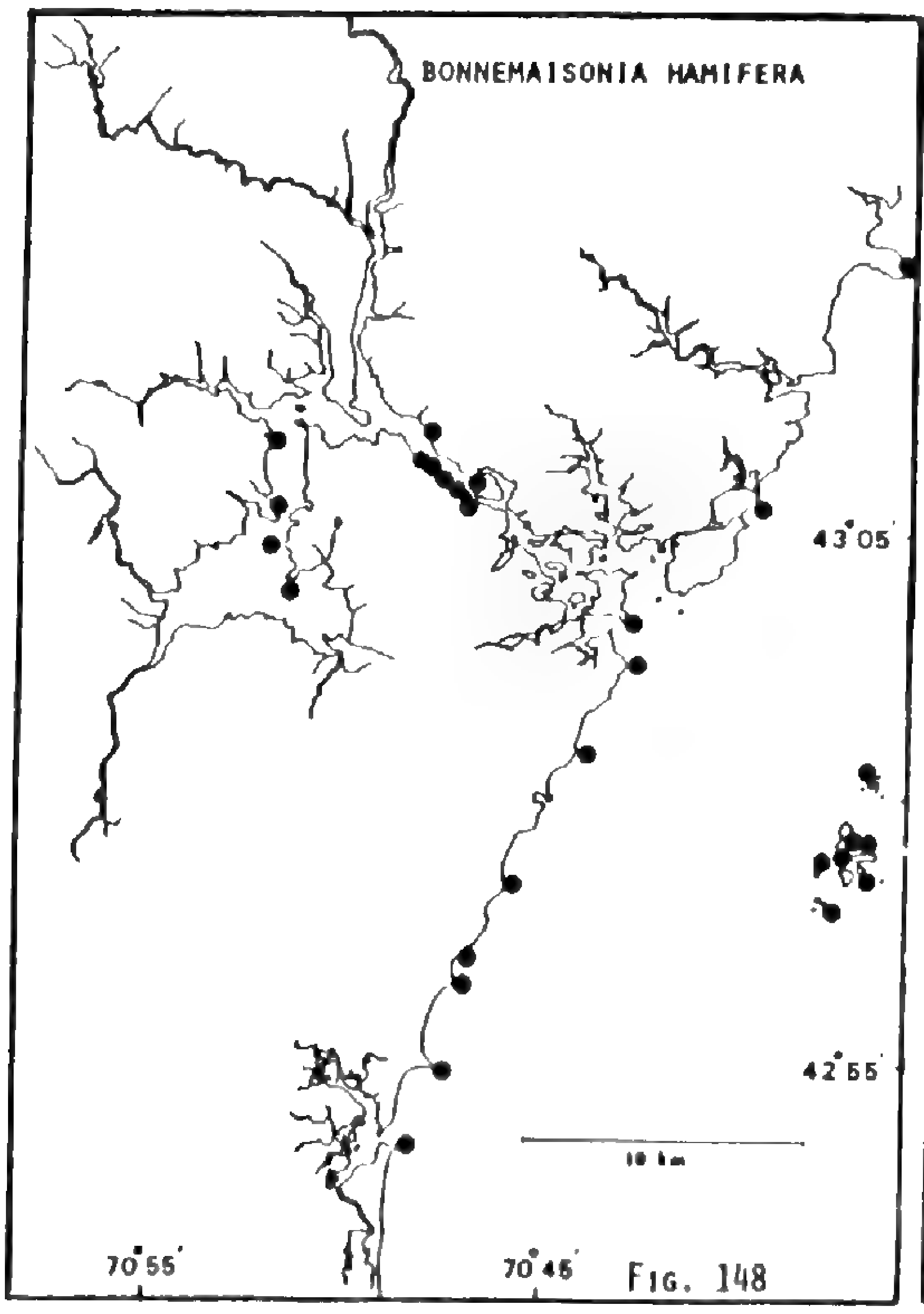


FIG. 148

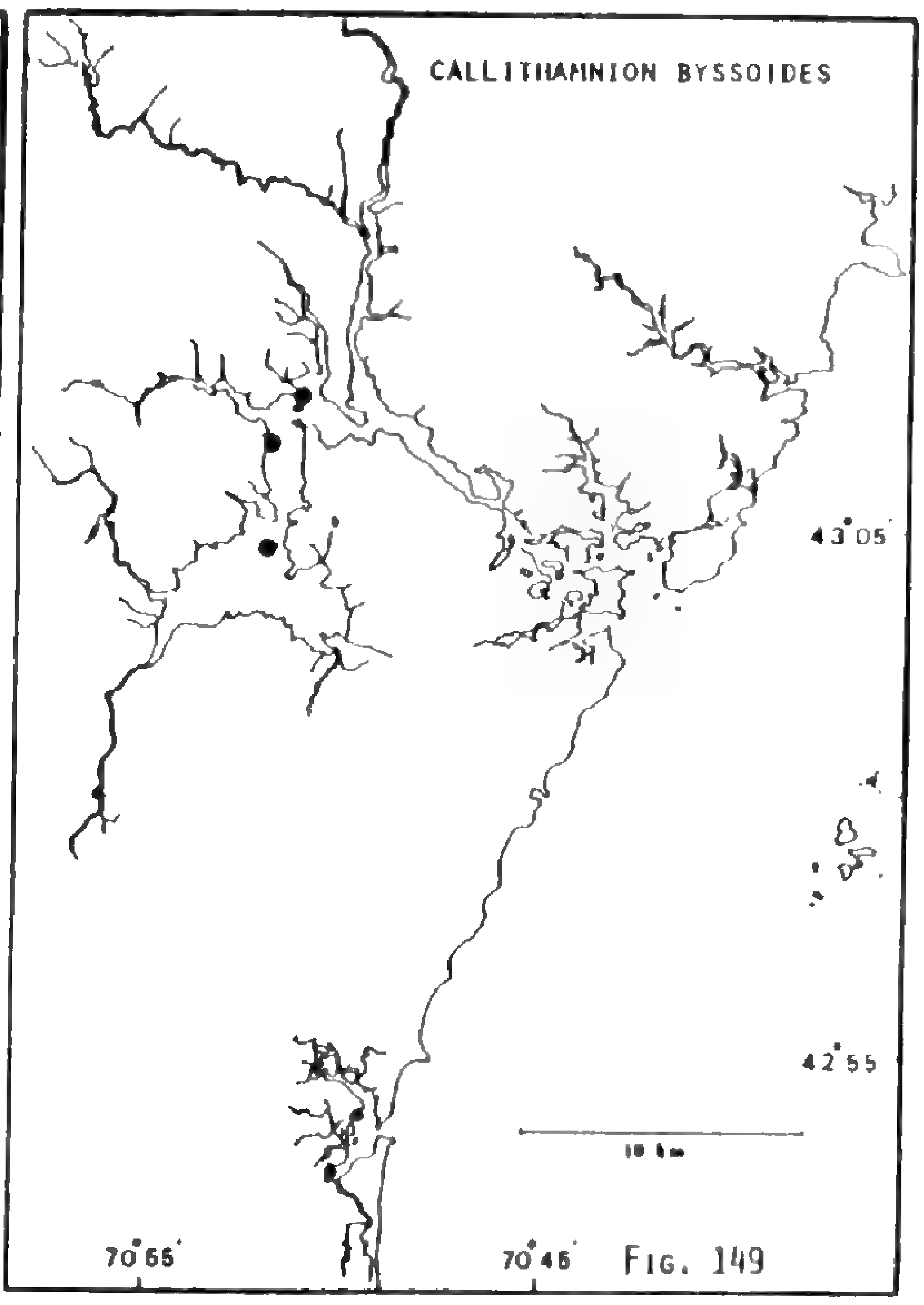


FIG. 149

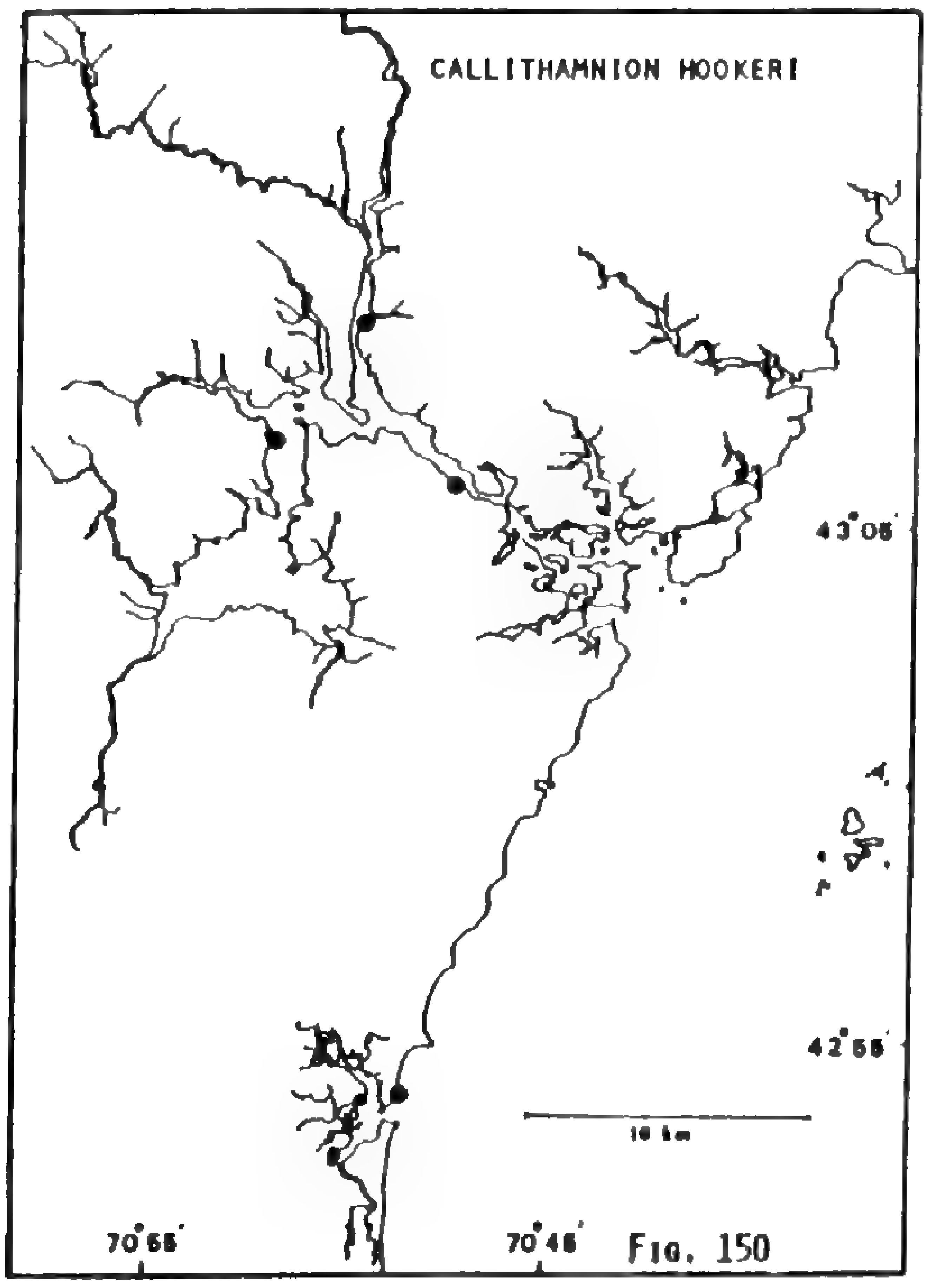


FIG. 150

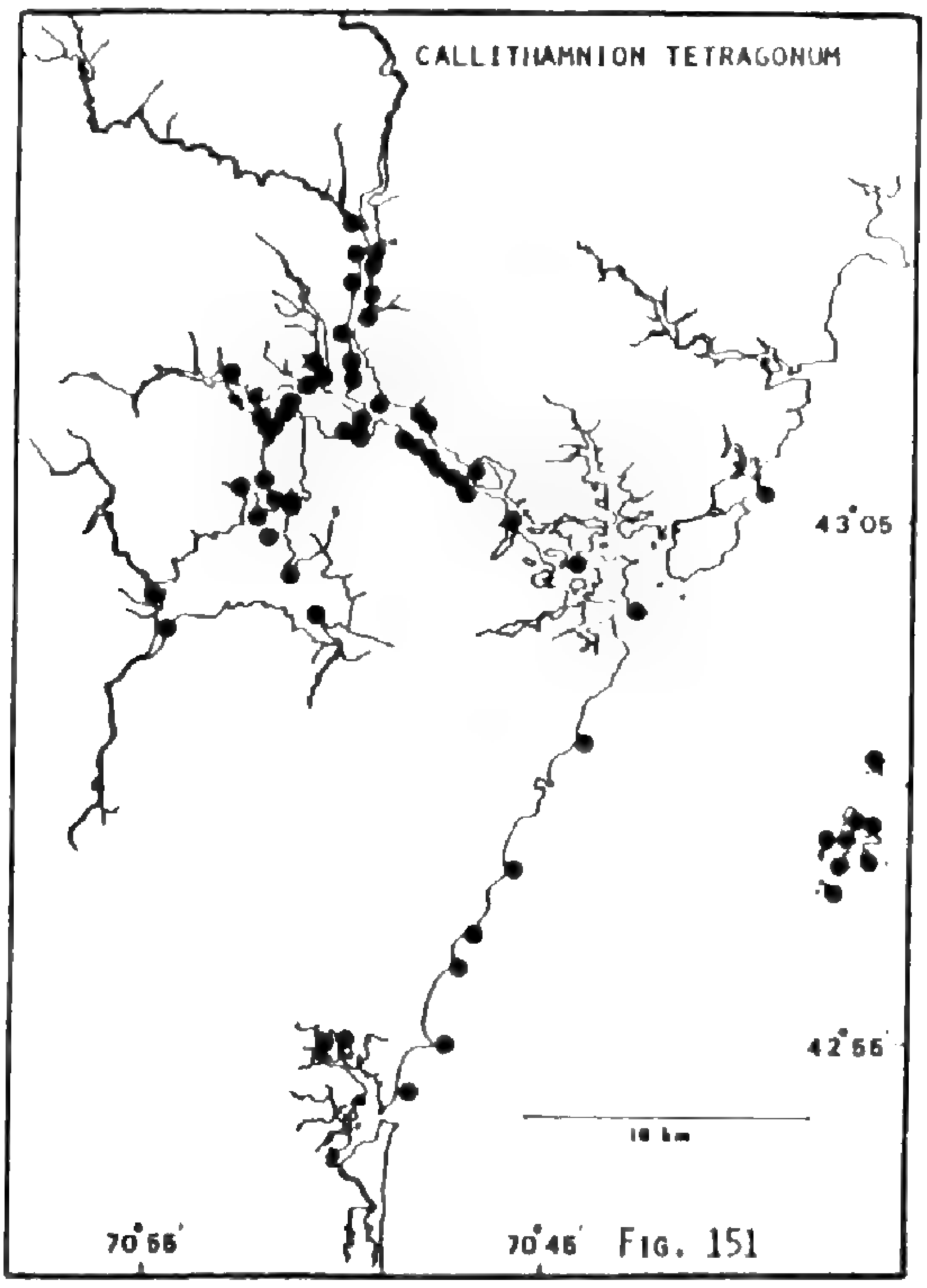


FIG. 151

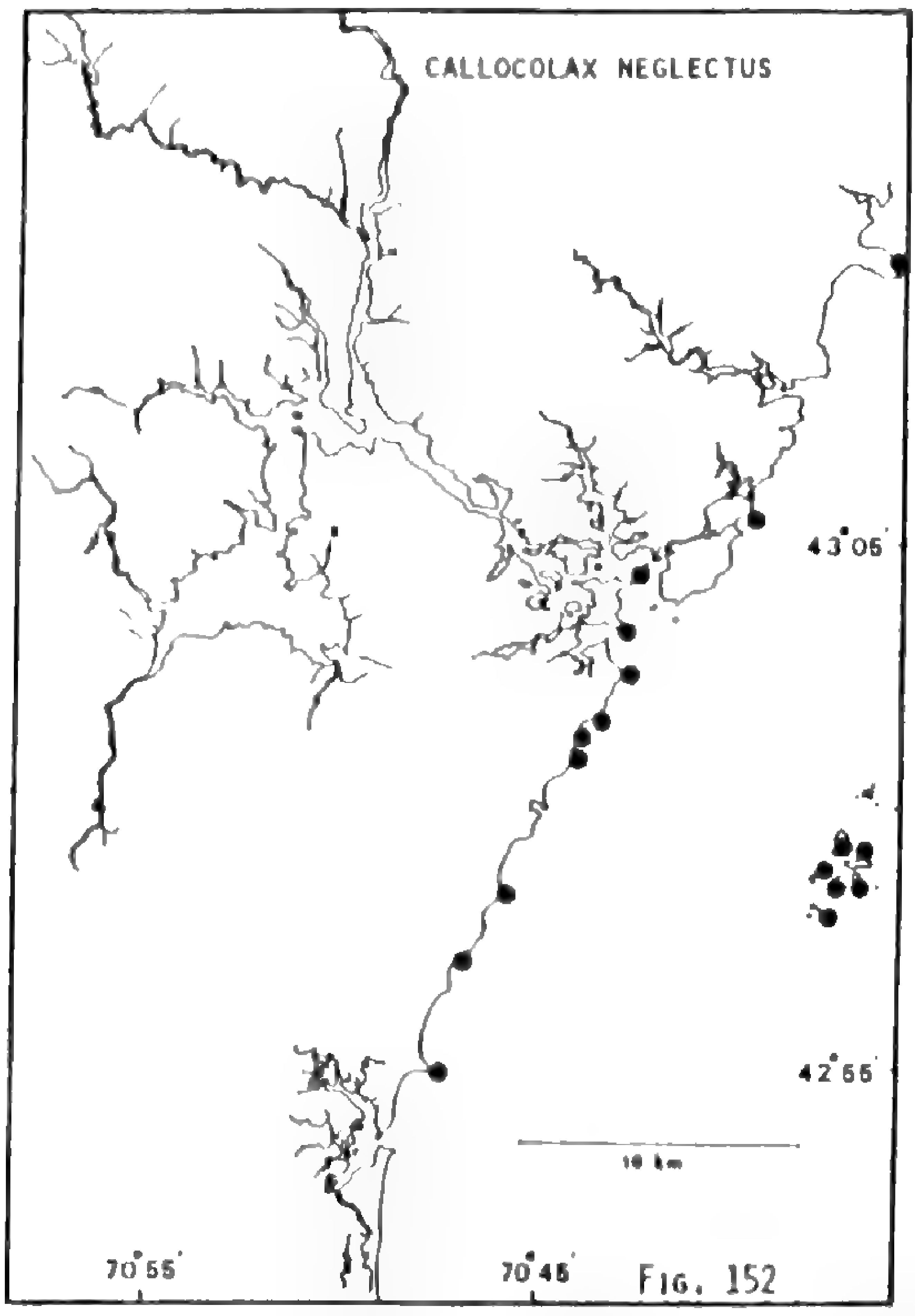


FIG. 152

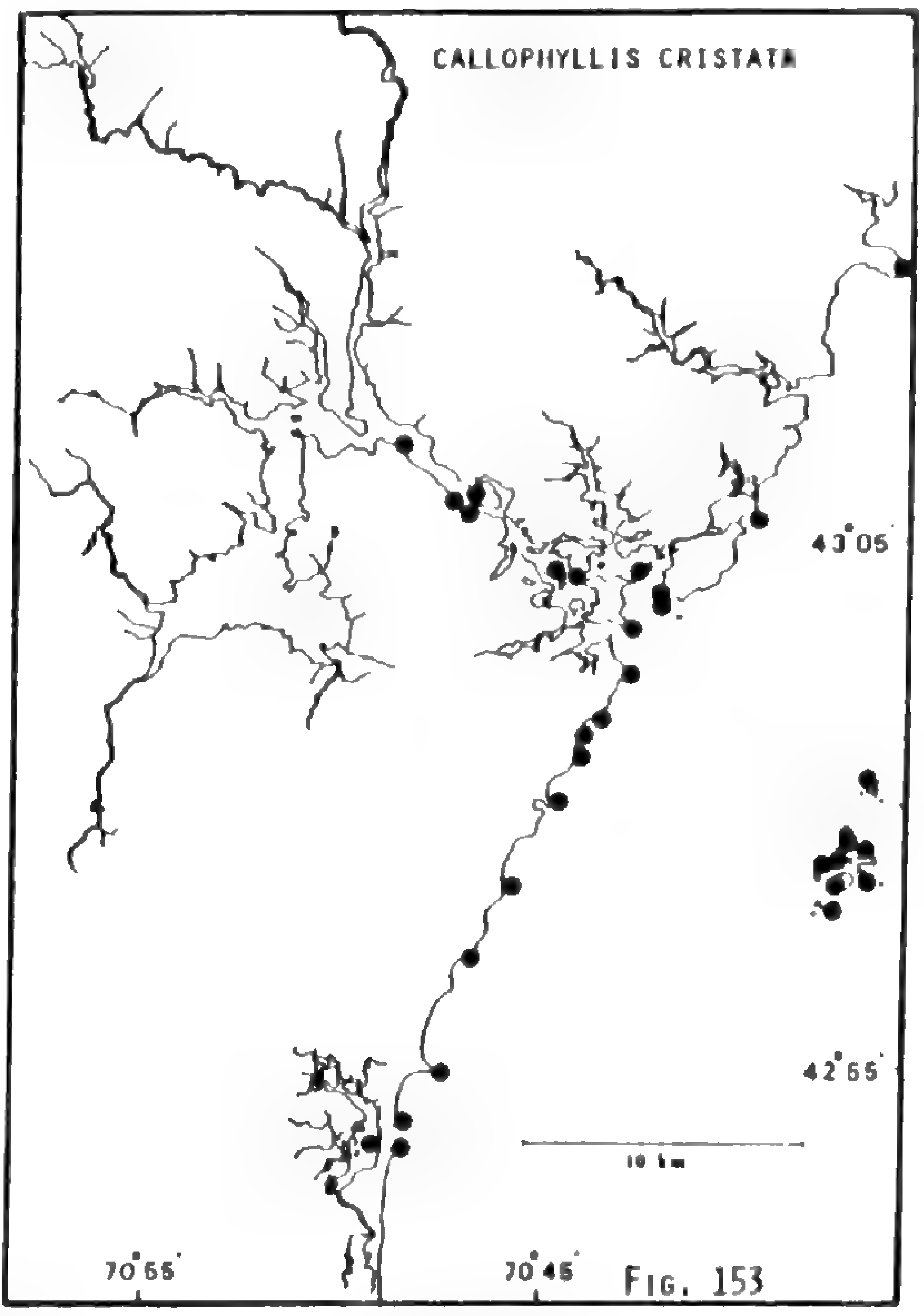


FIG. 153

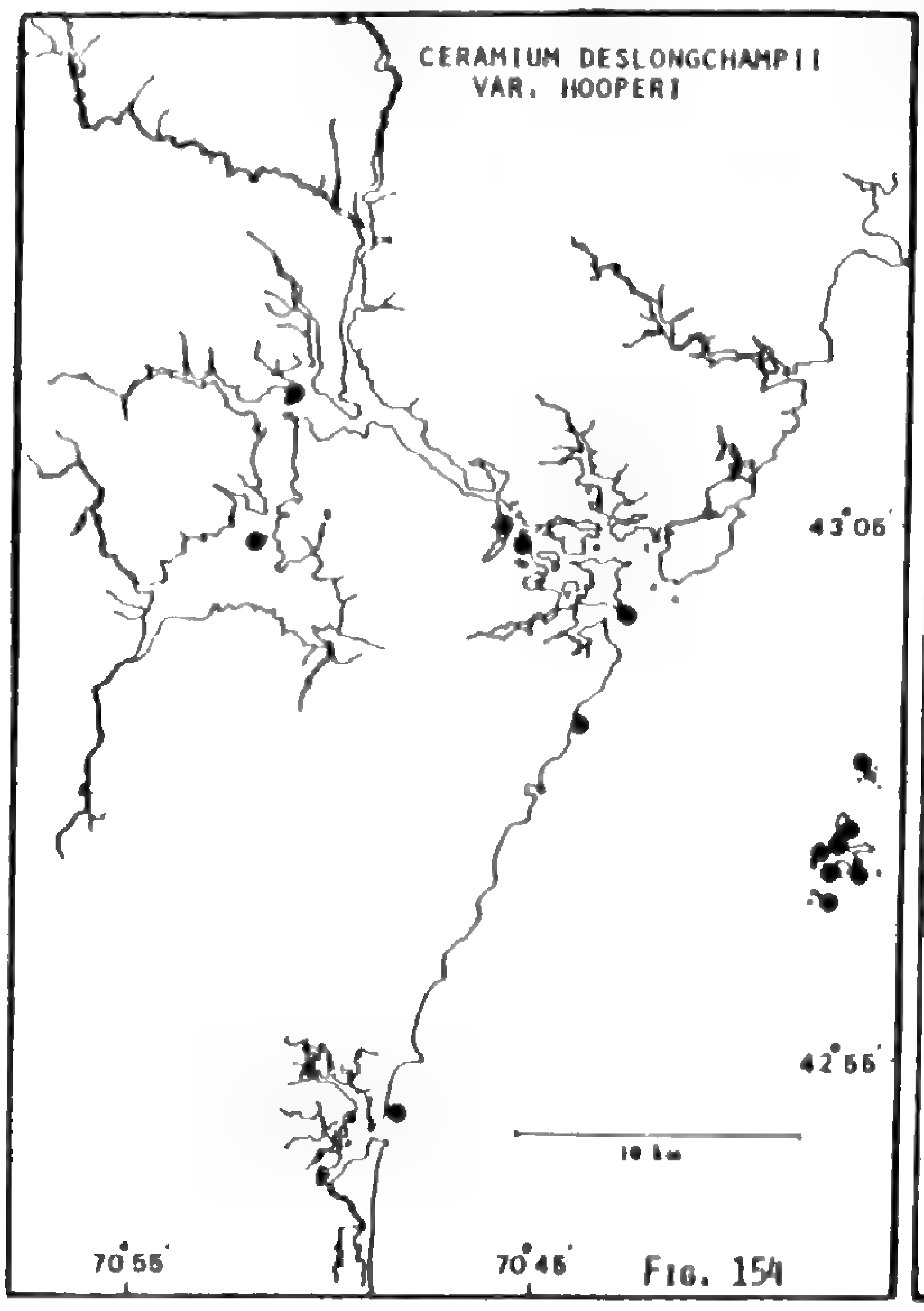


FIG. 154

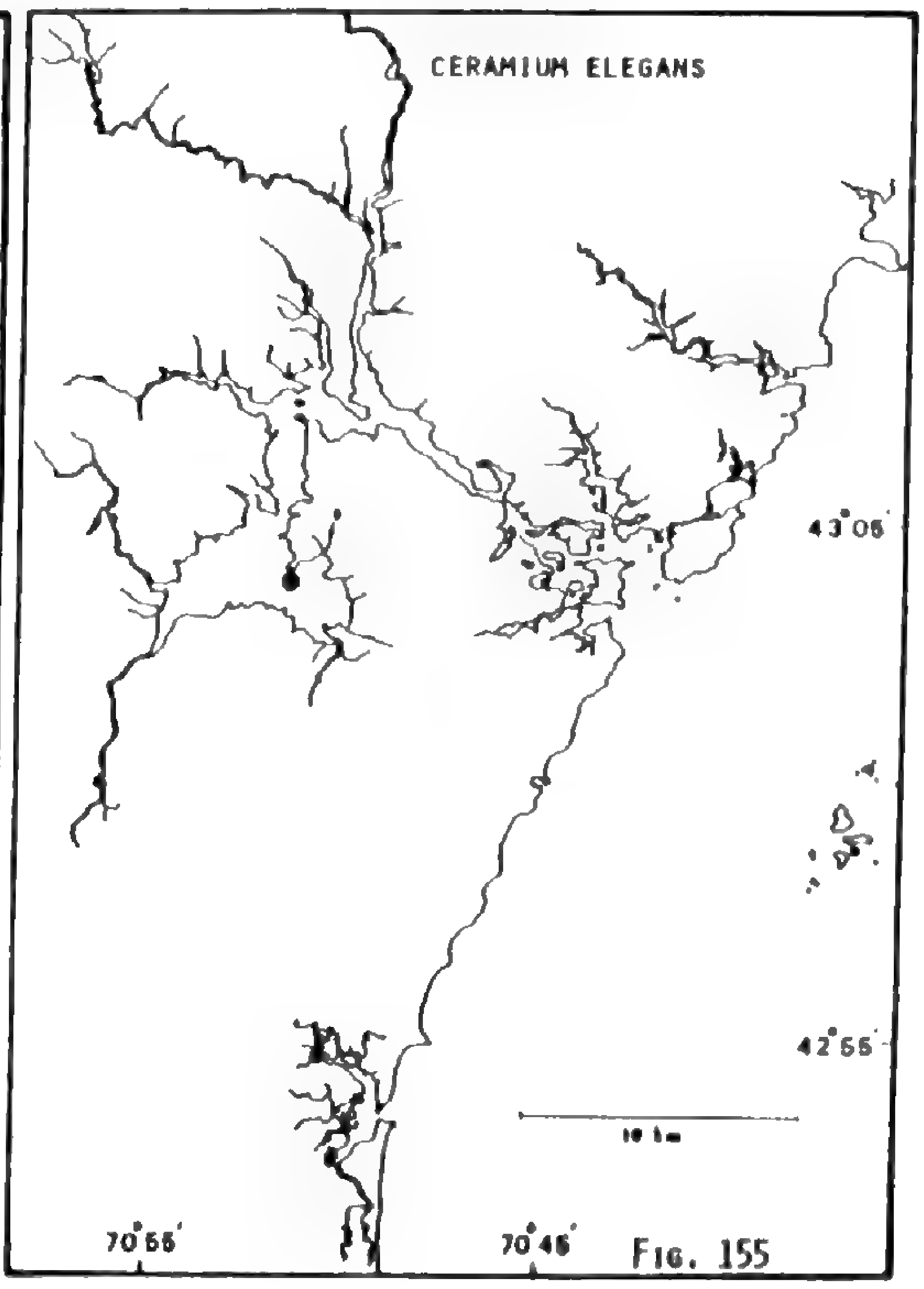


FIG. 155

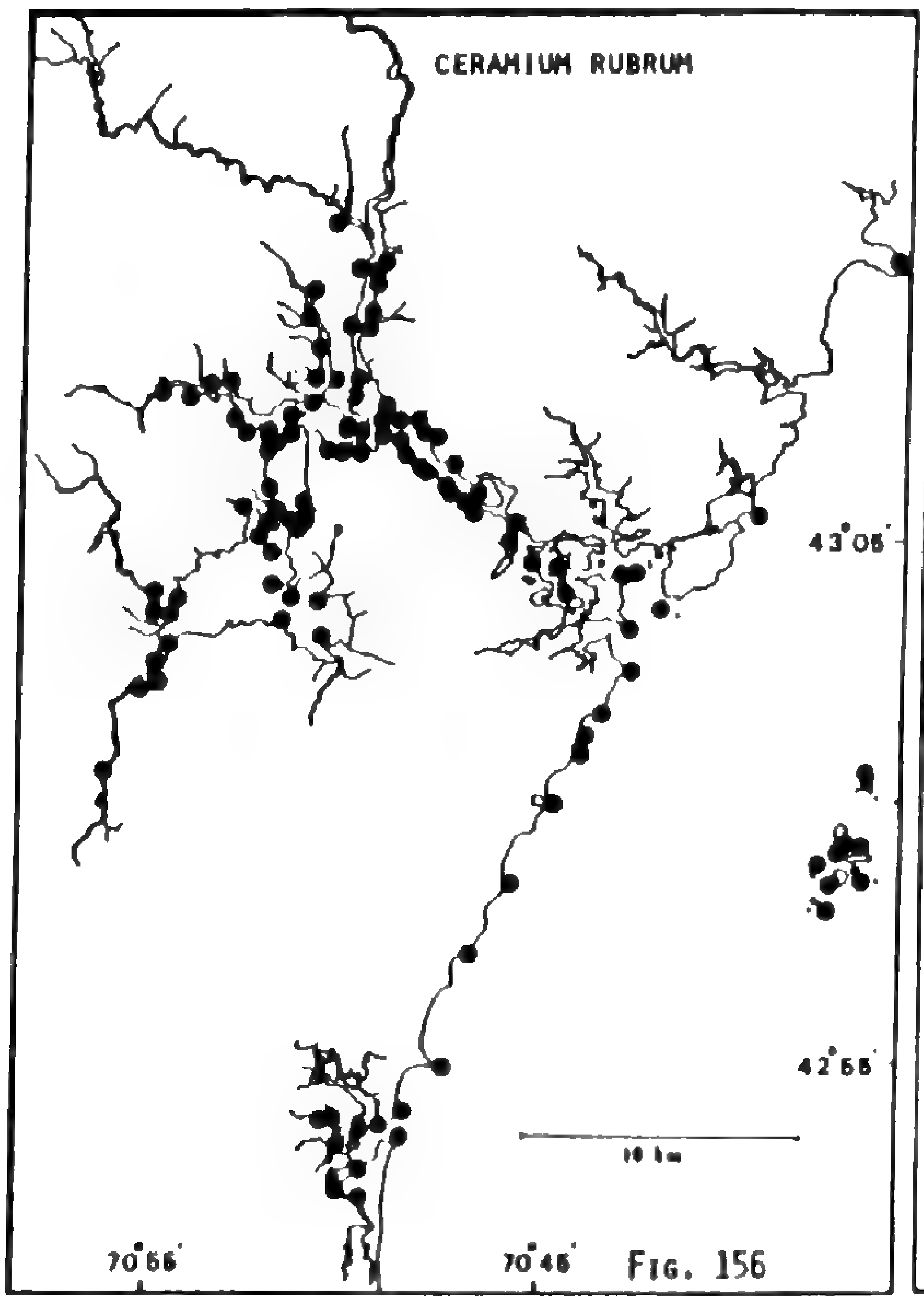


FIG. 156

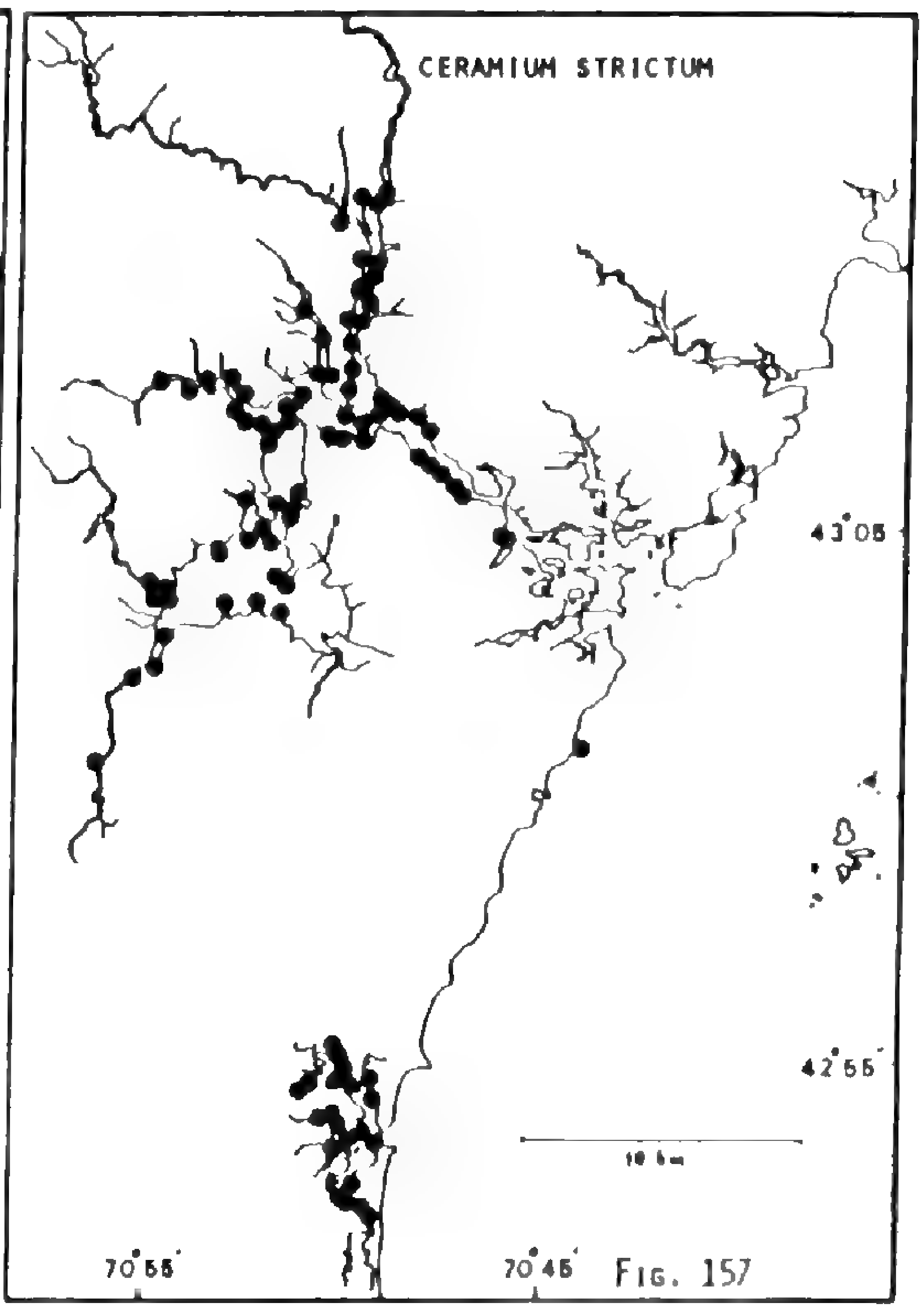


FIG. 157

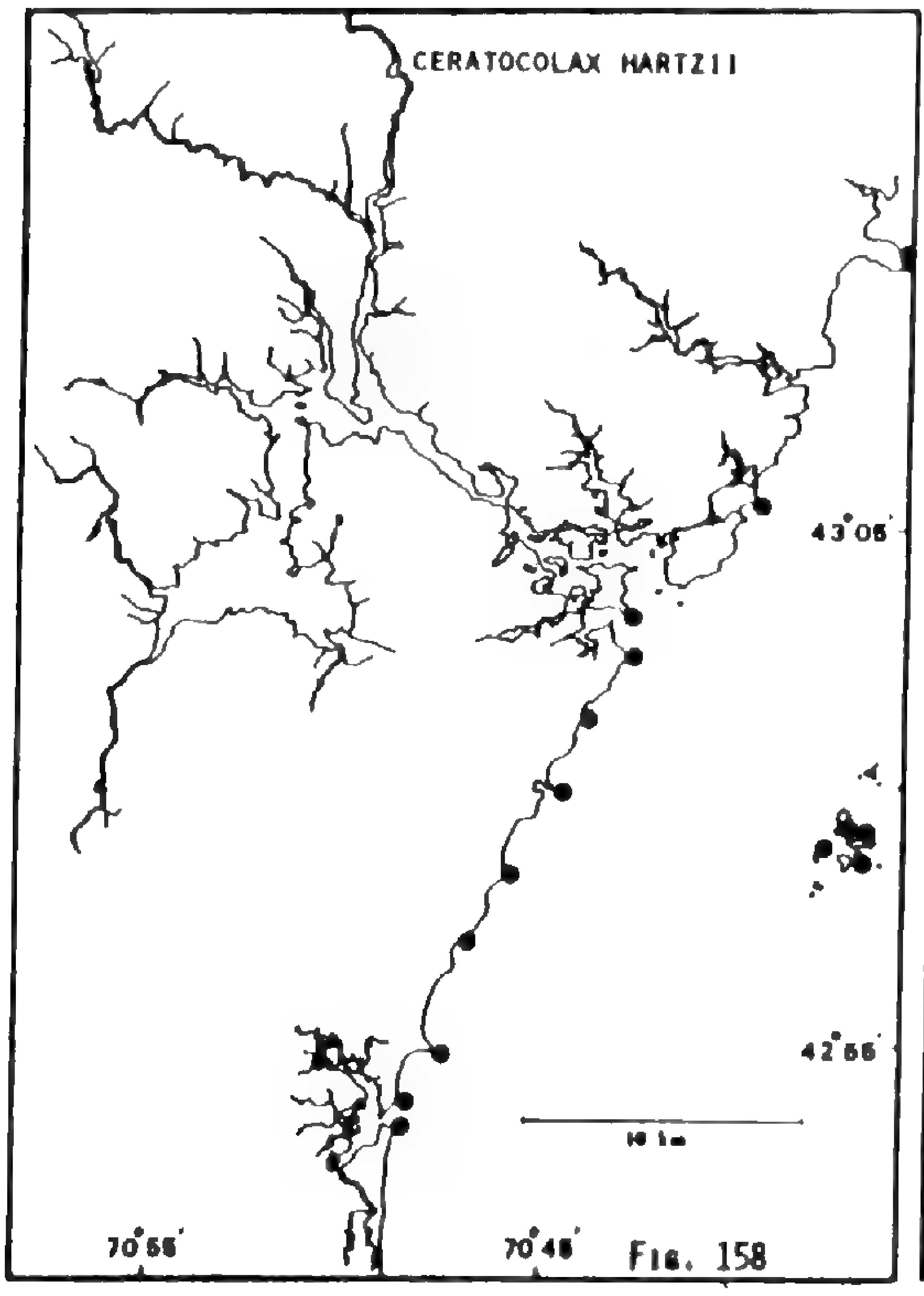


FIG. 158

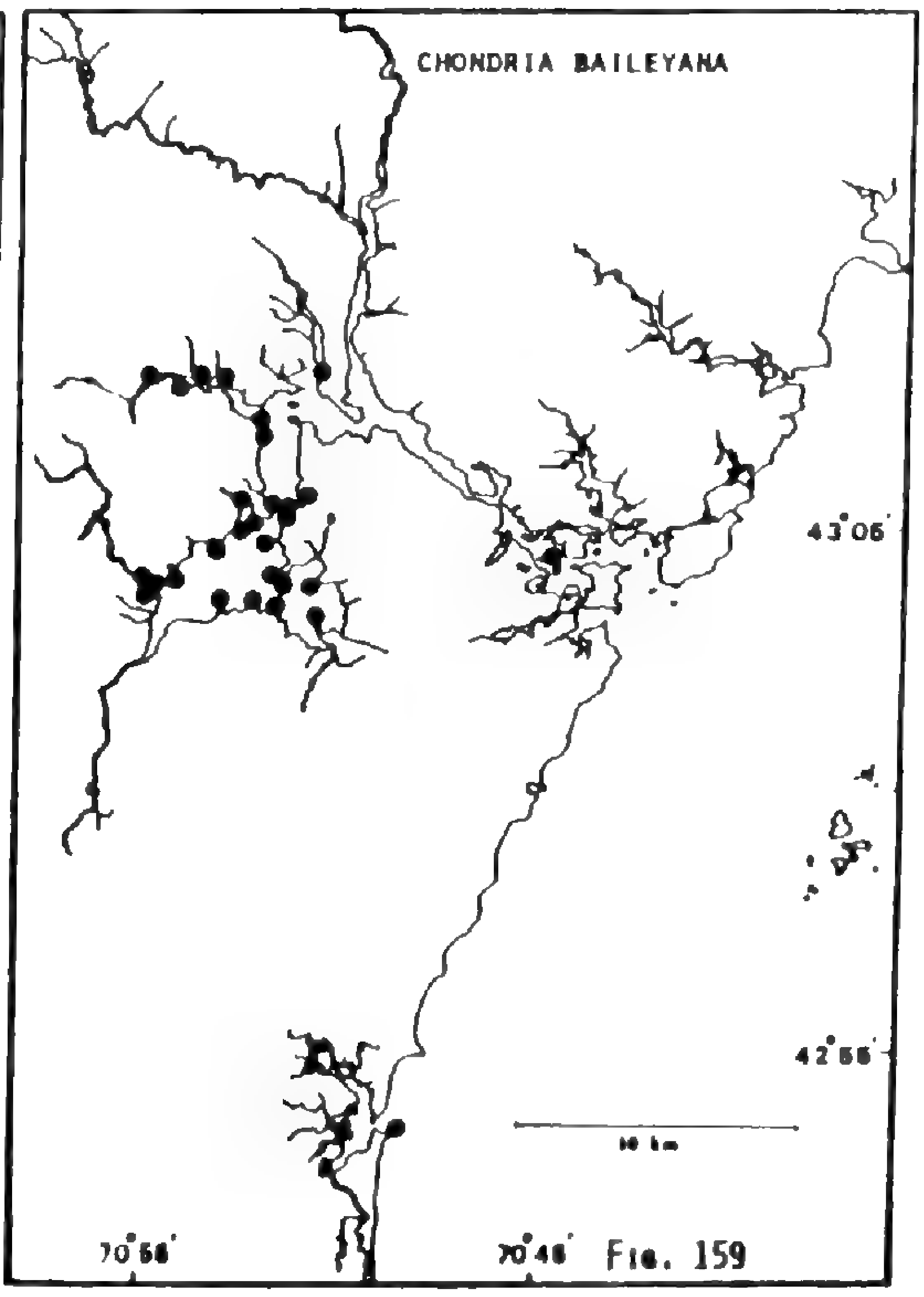


FIG. 159

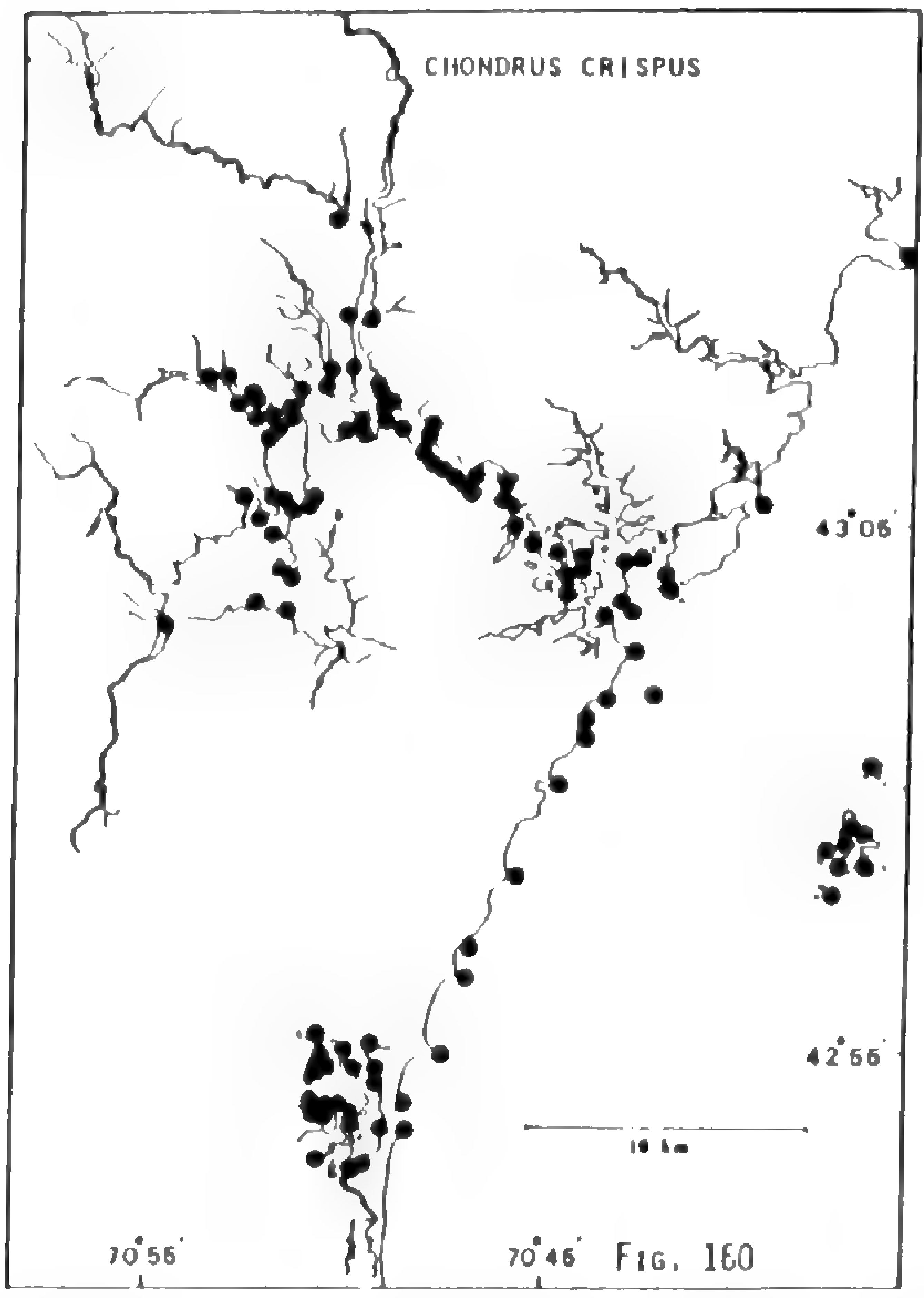


FIG. 160

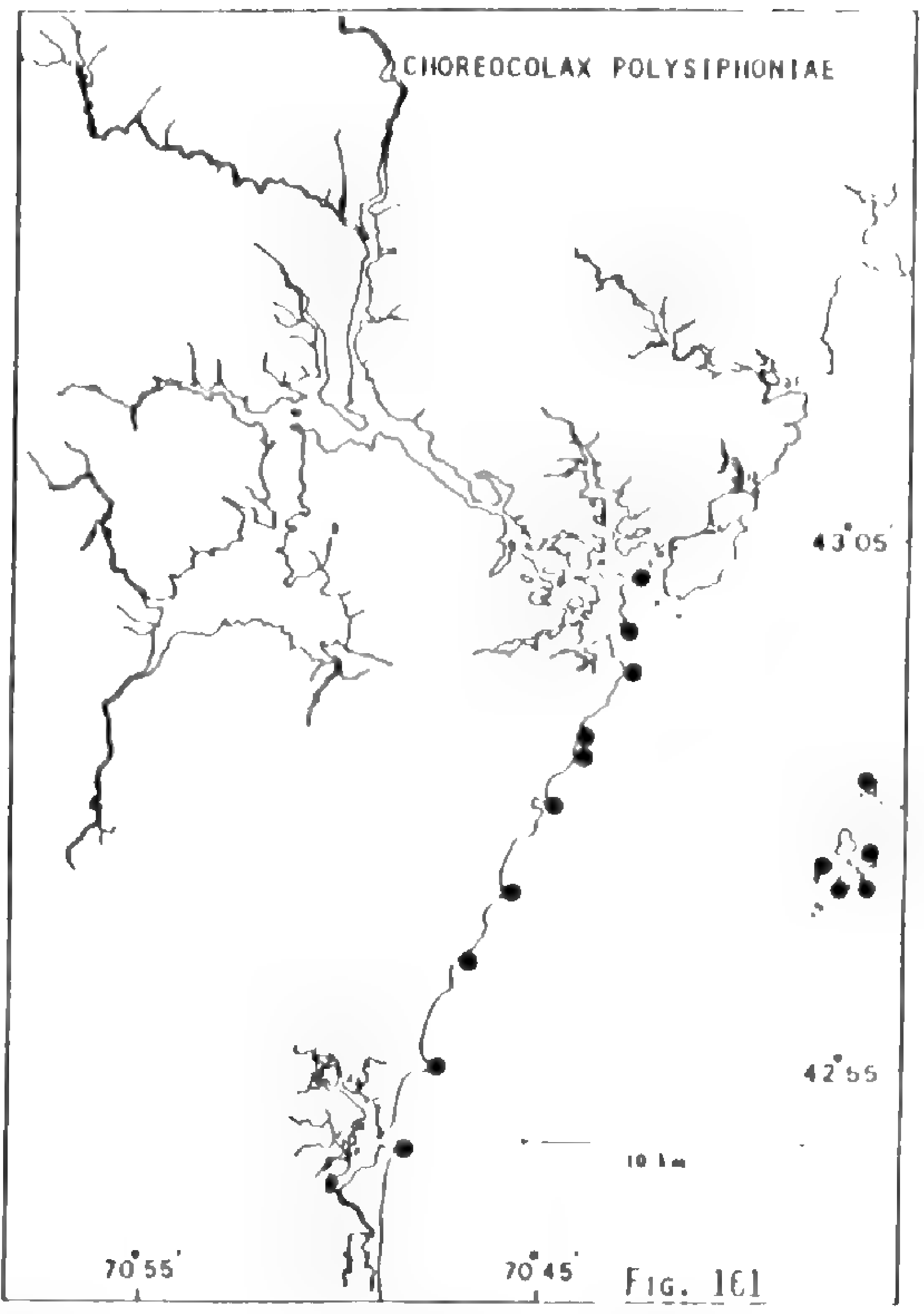


FIG. 161

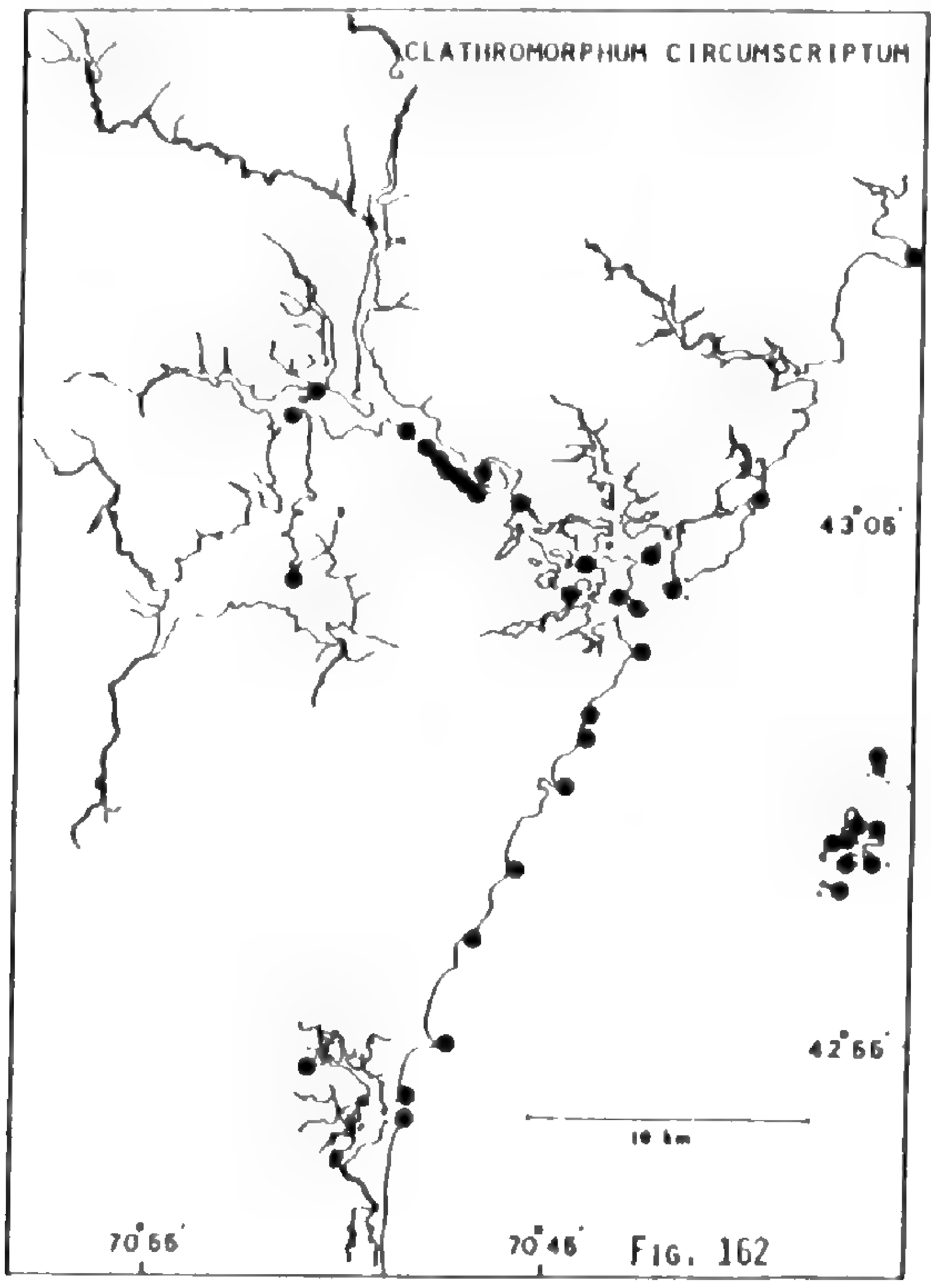


FIG. 162

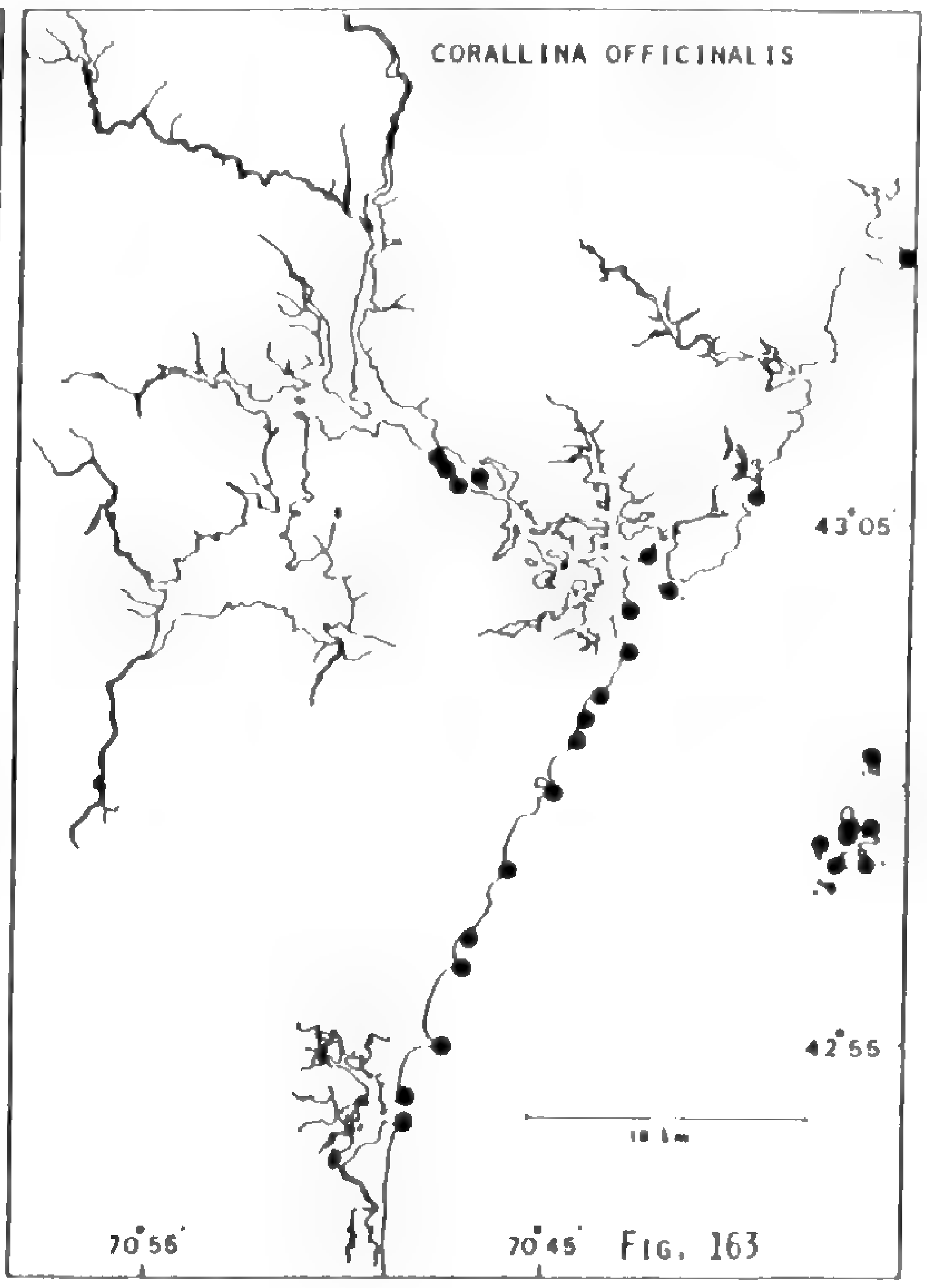


FIG. 163

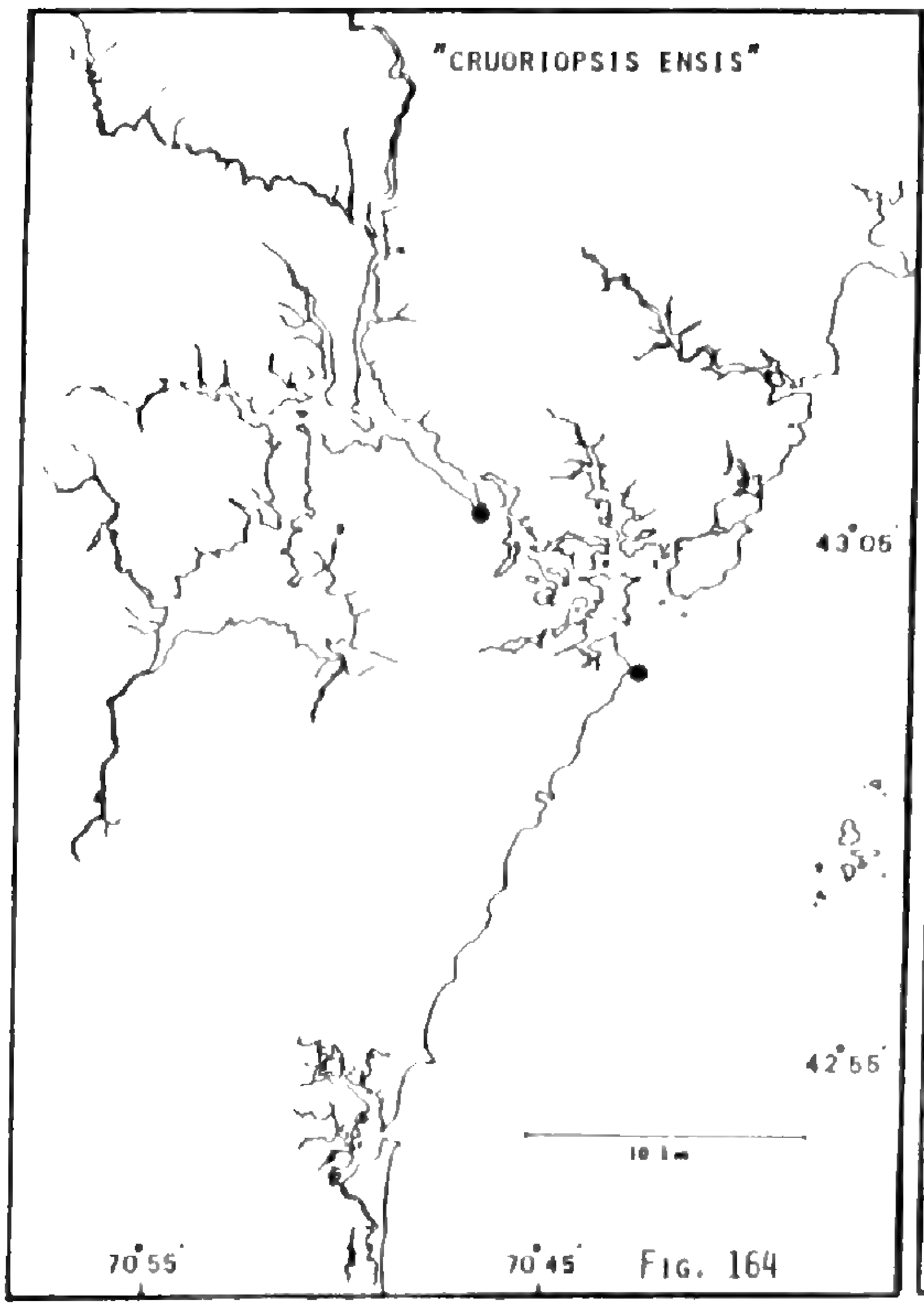

"CRUORIOPSIS ENSIS"

FIG. 164

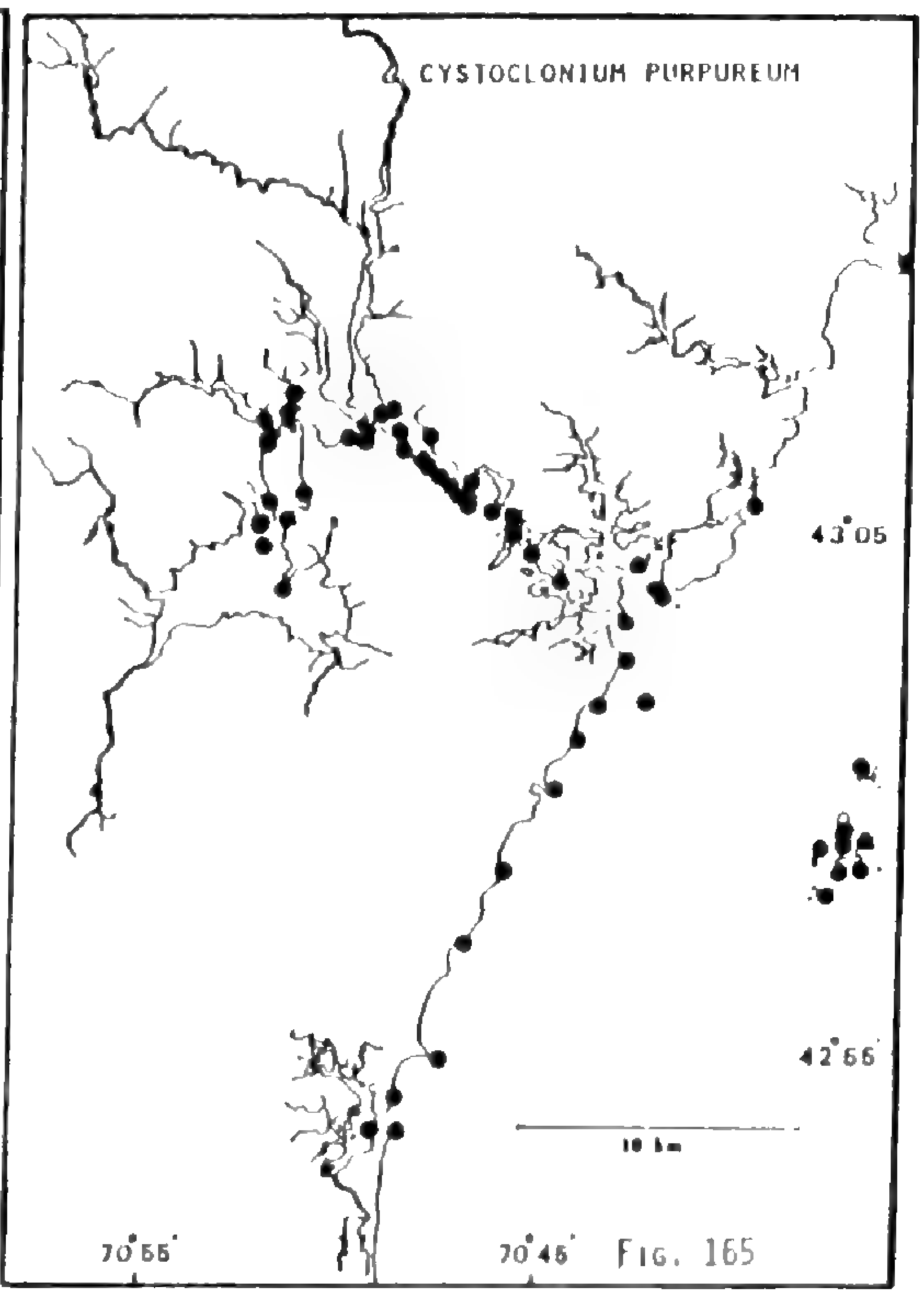

CYSTOCLONIUM PURPUREUM

FIG. 165

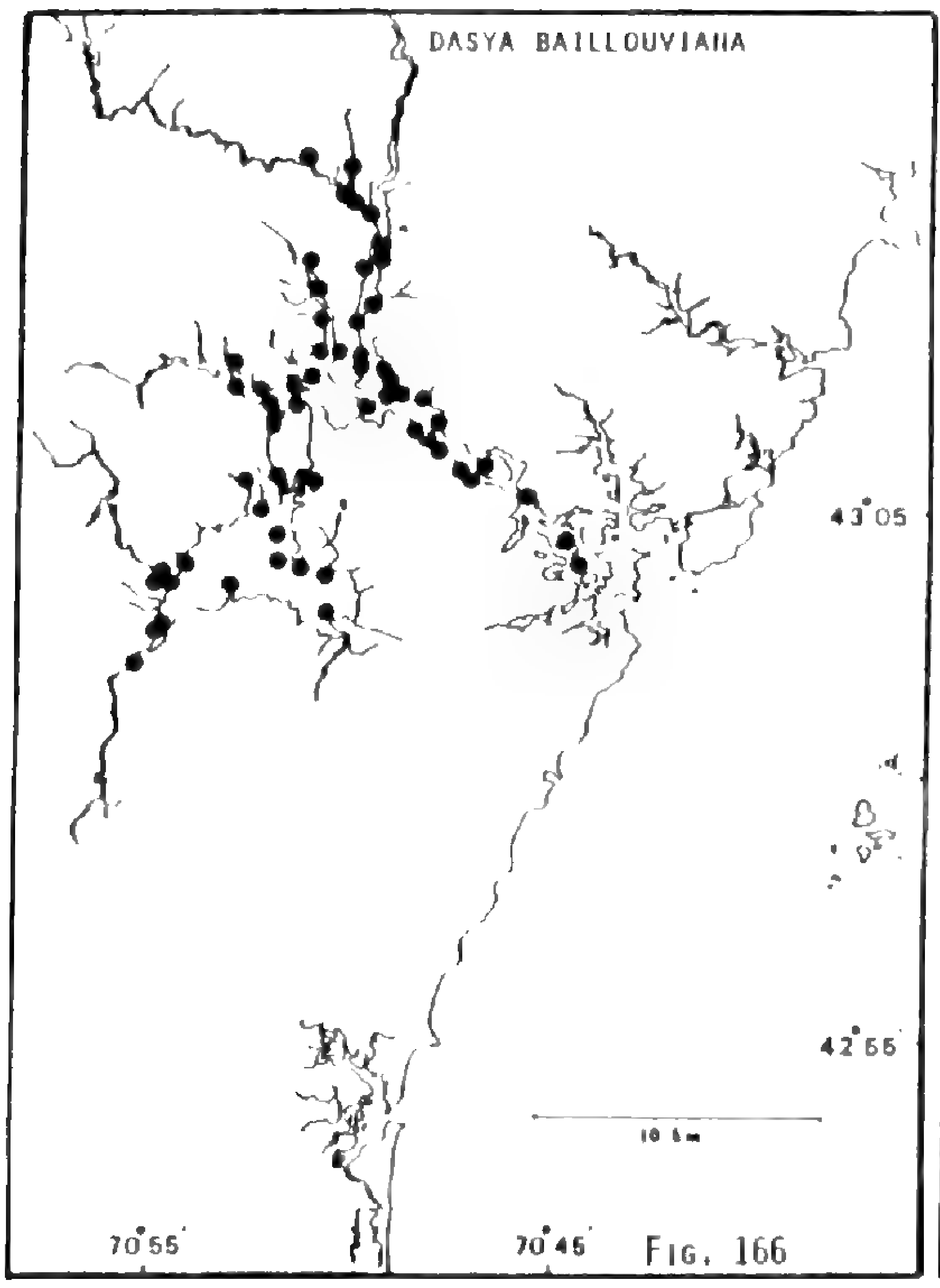

DASYA BAILLOUVIANA

FIG. 166

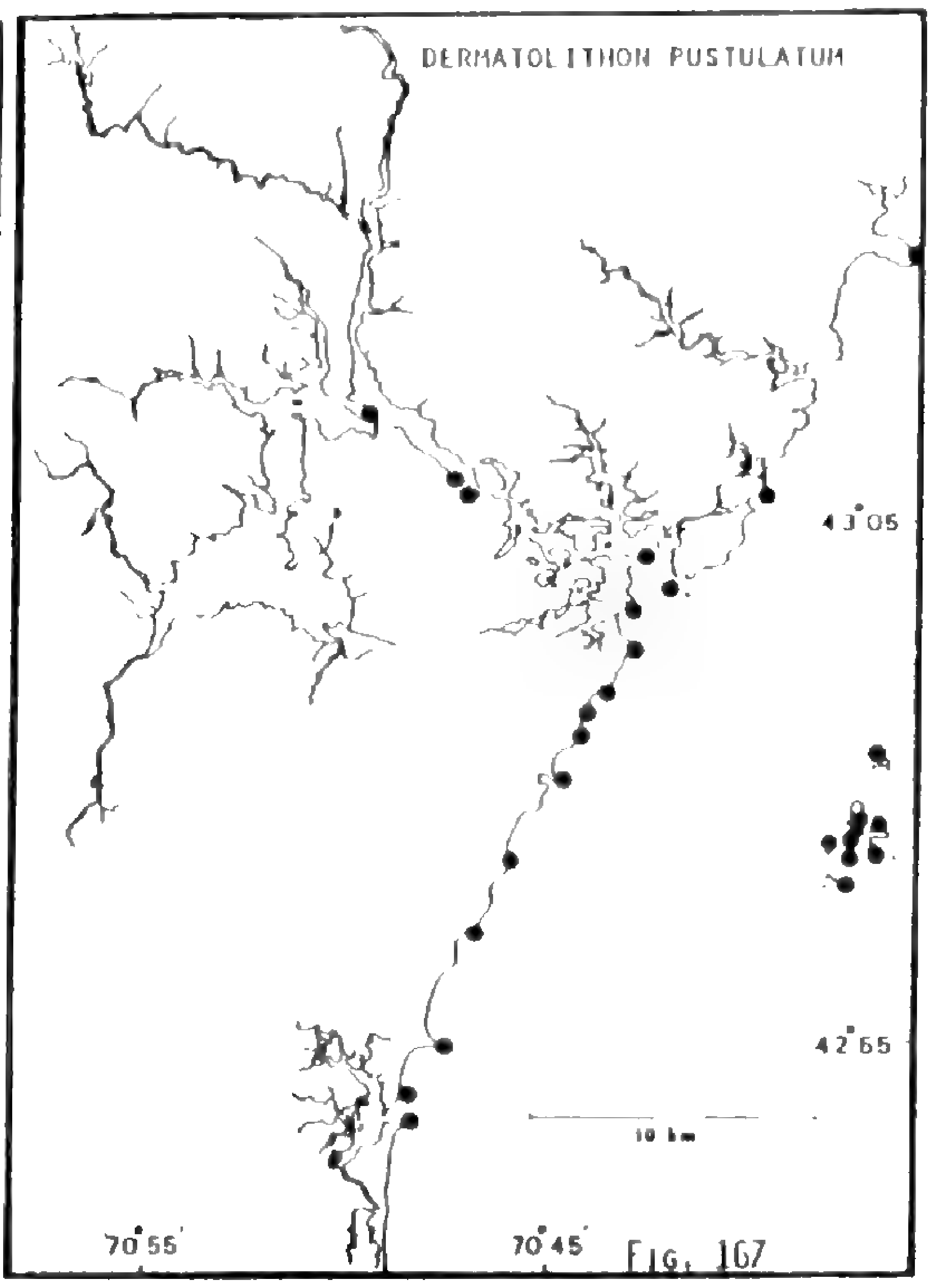

DERMATOLITHON PUSTULATUM

FIG. 167

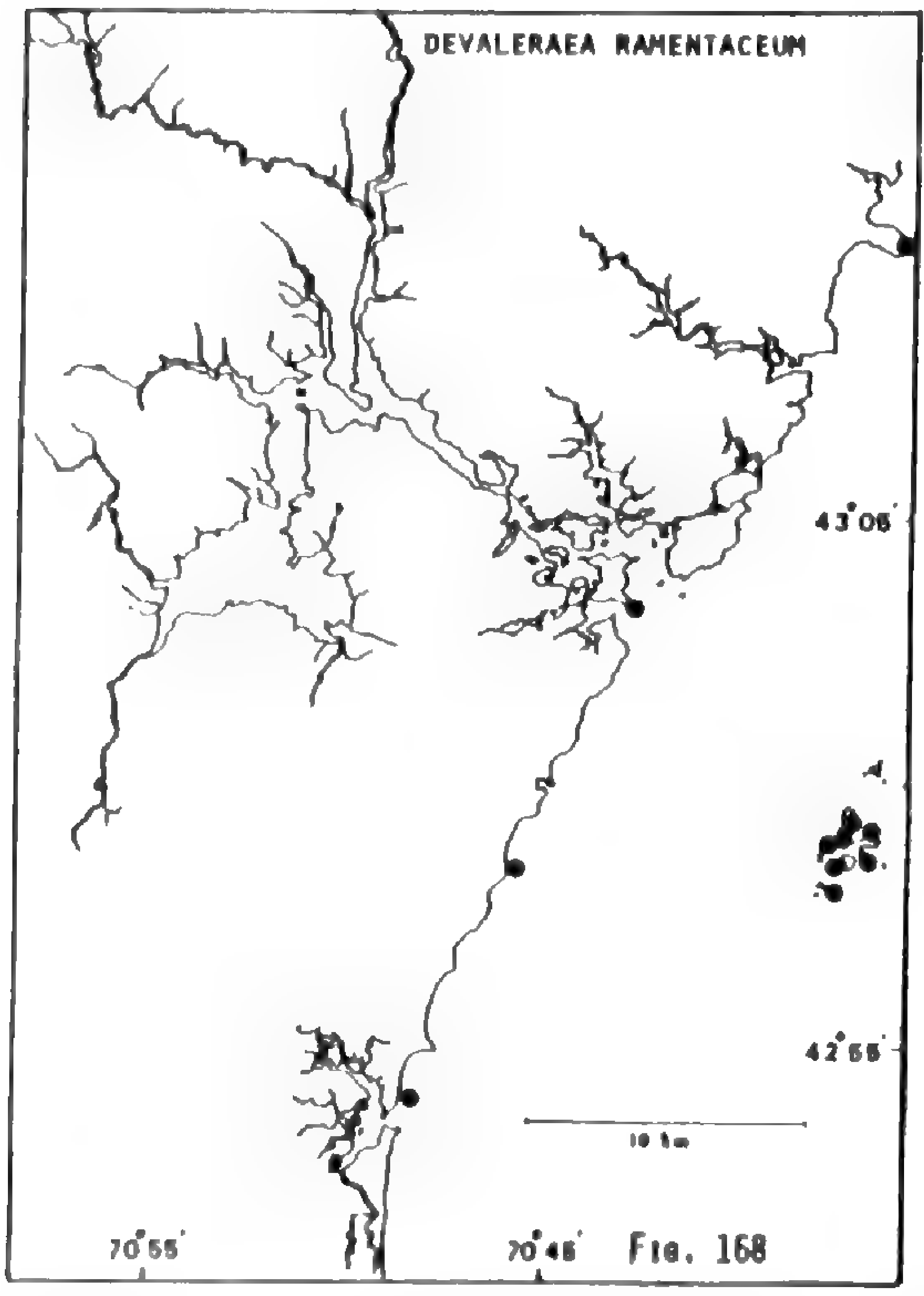


FIG. 168

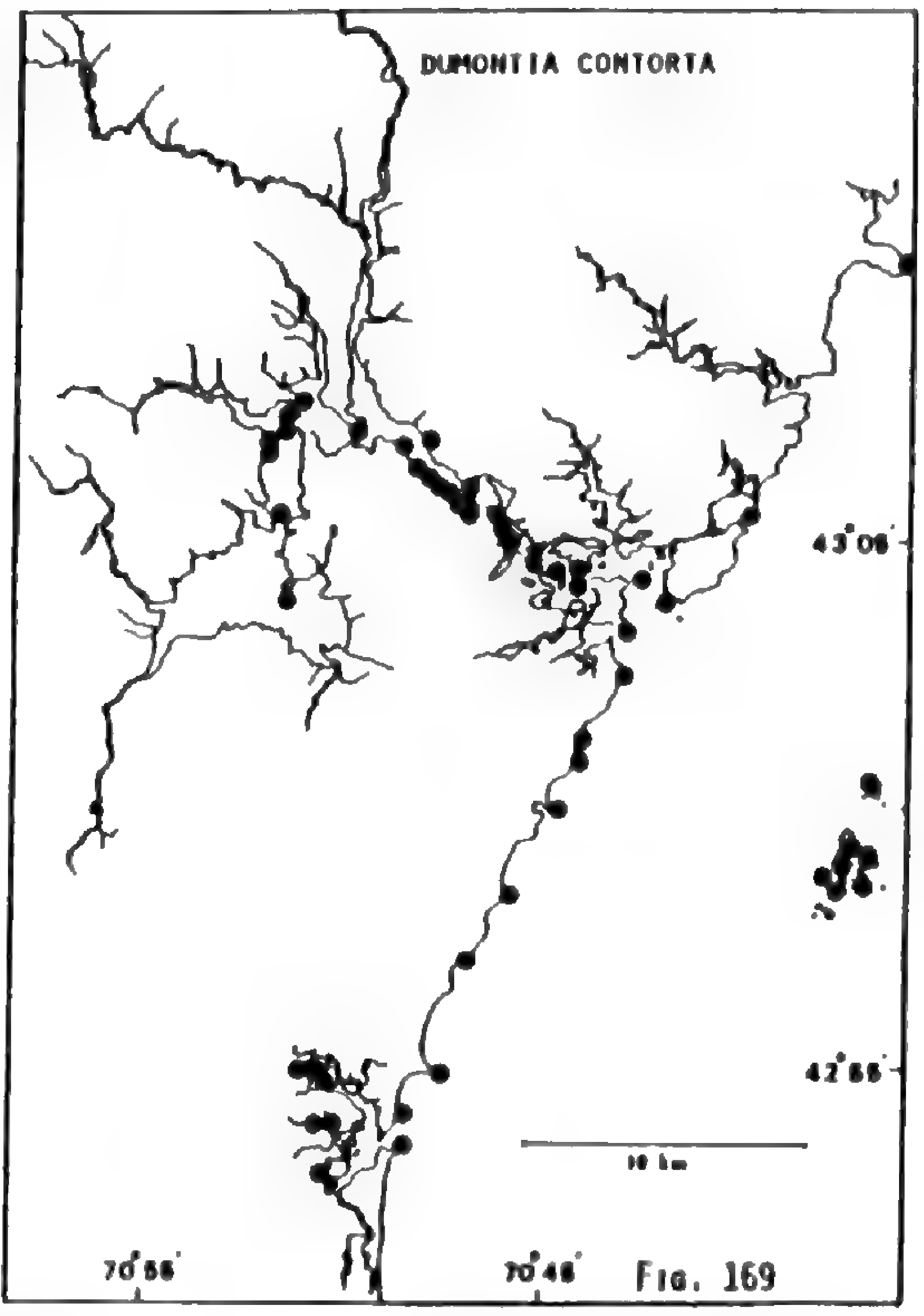


FIG. 169

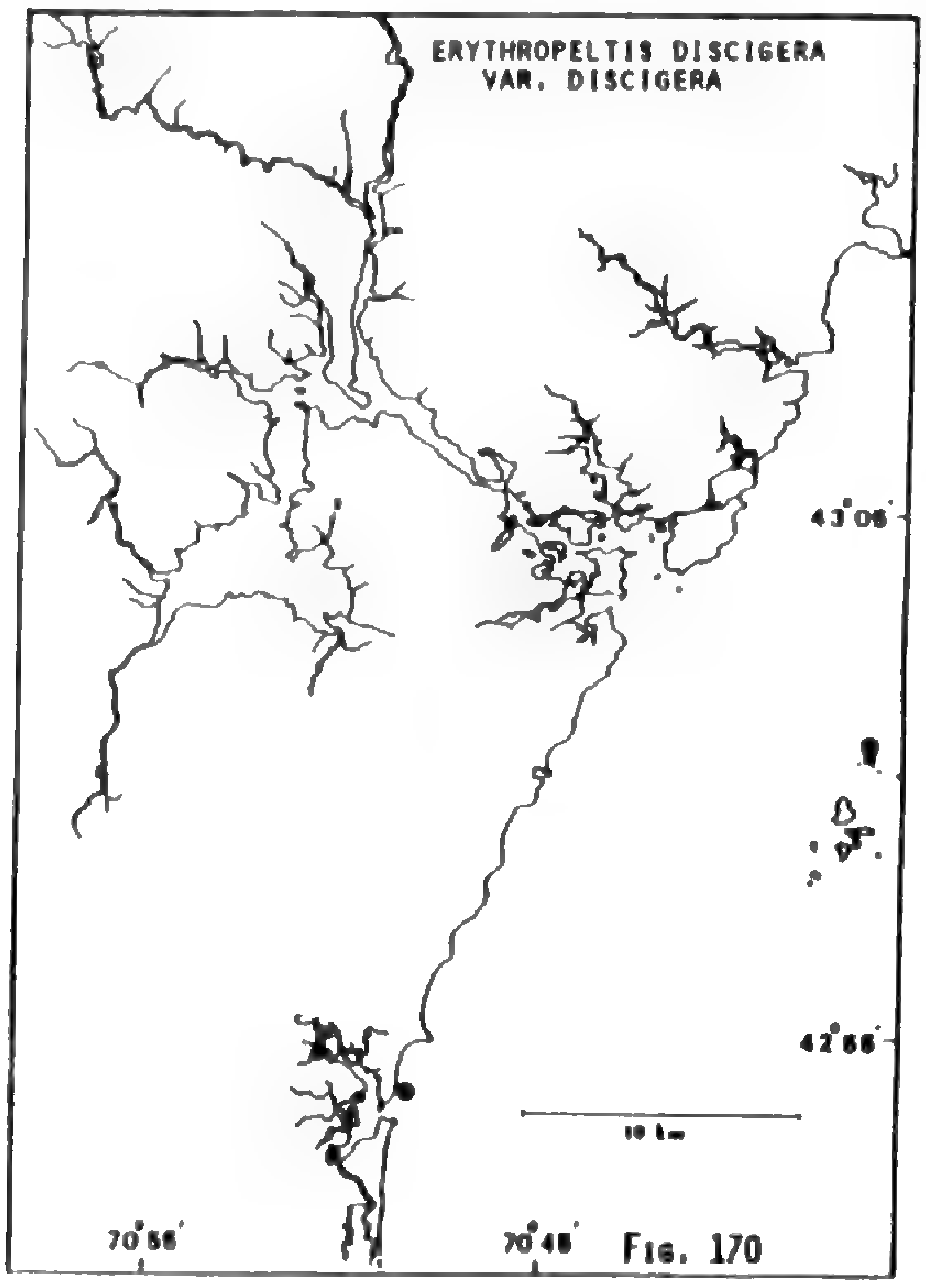


FIG. 170

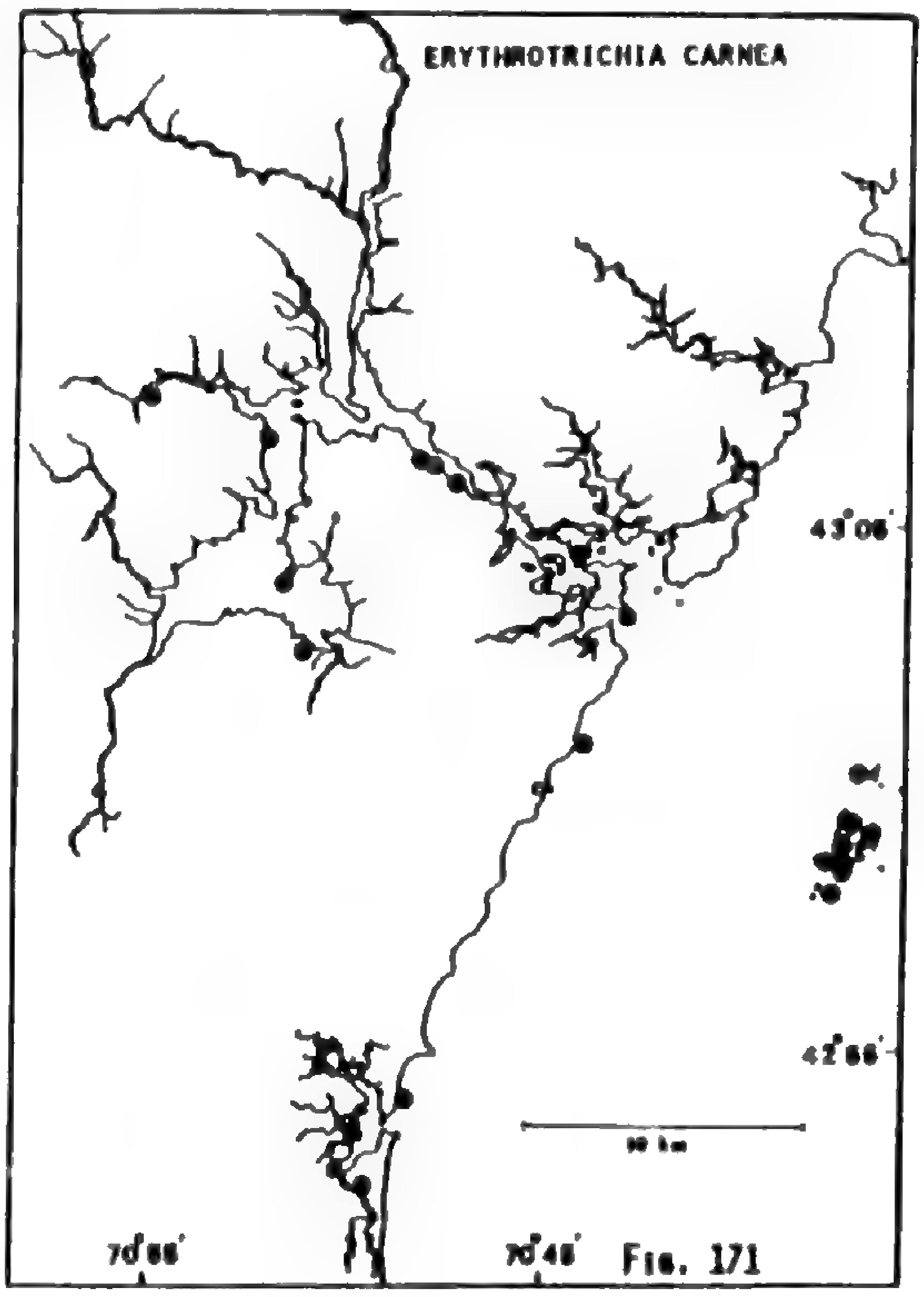


FIG. 171

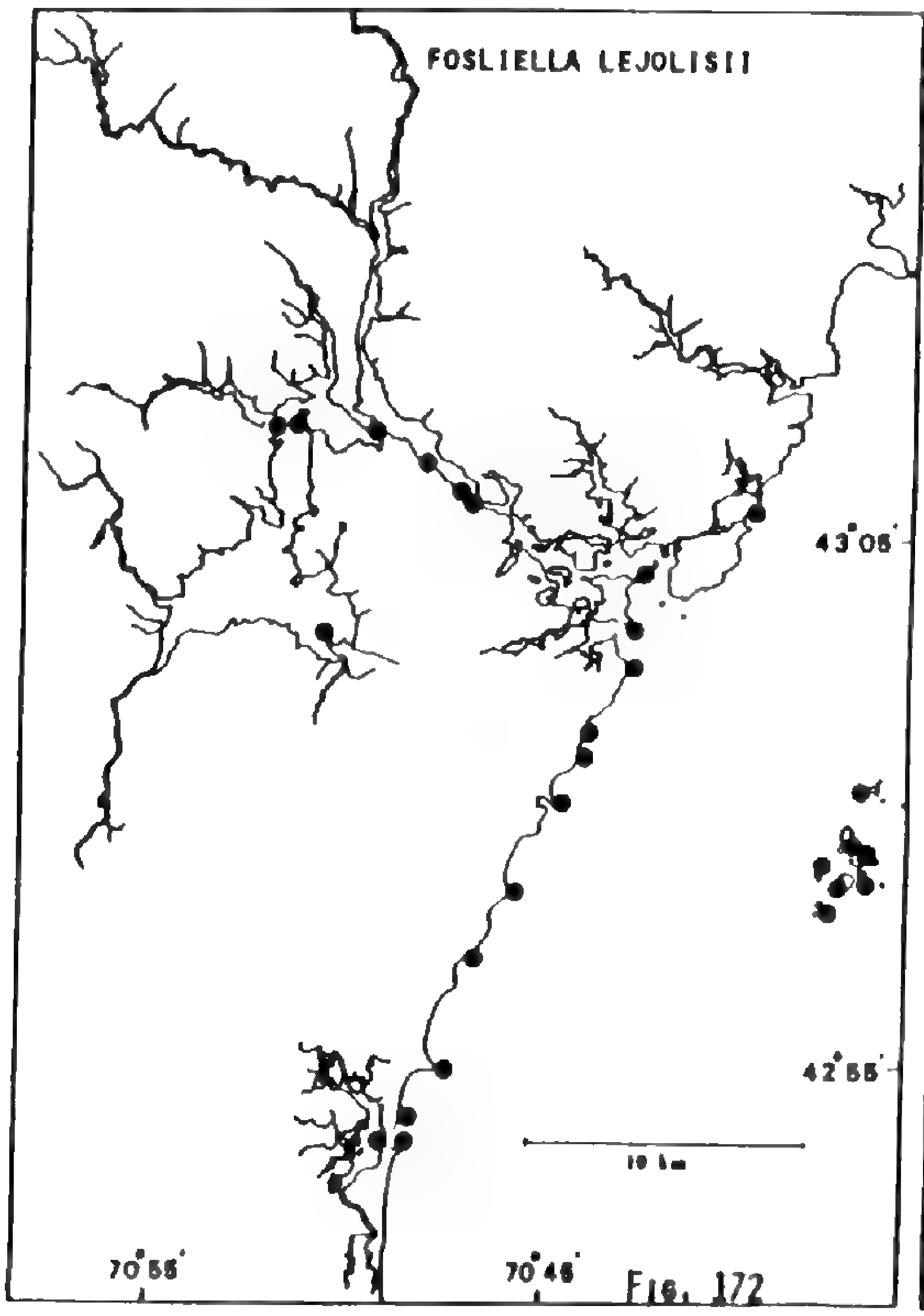


Fig. 172

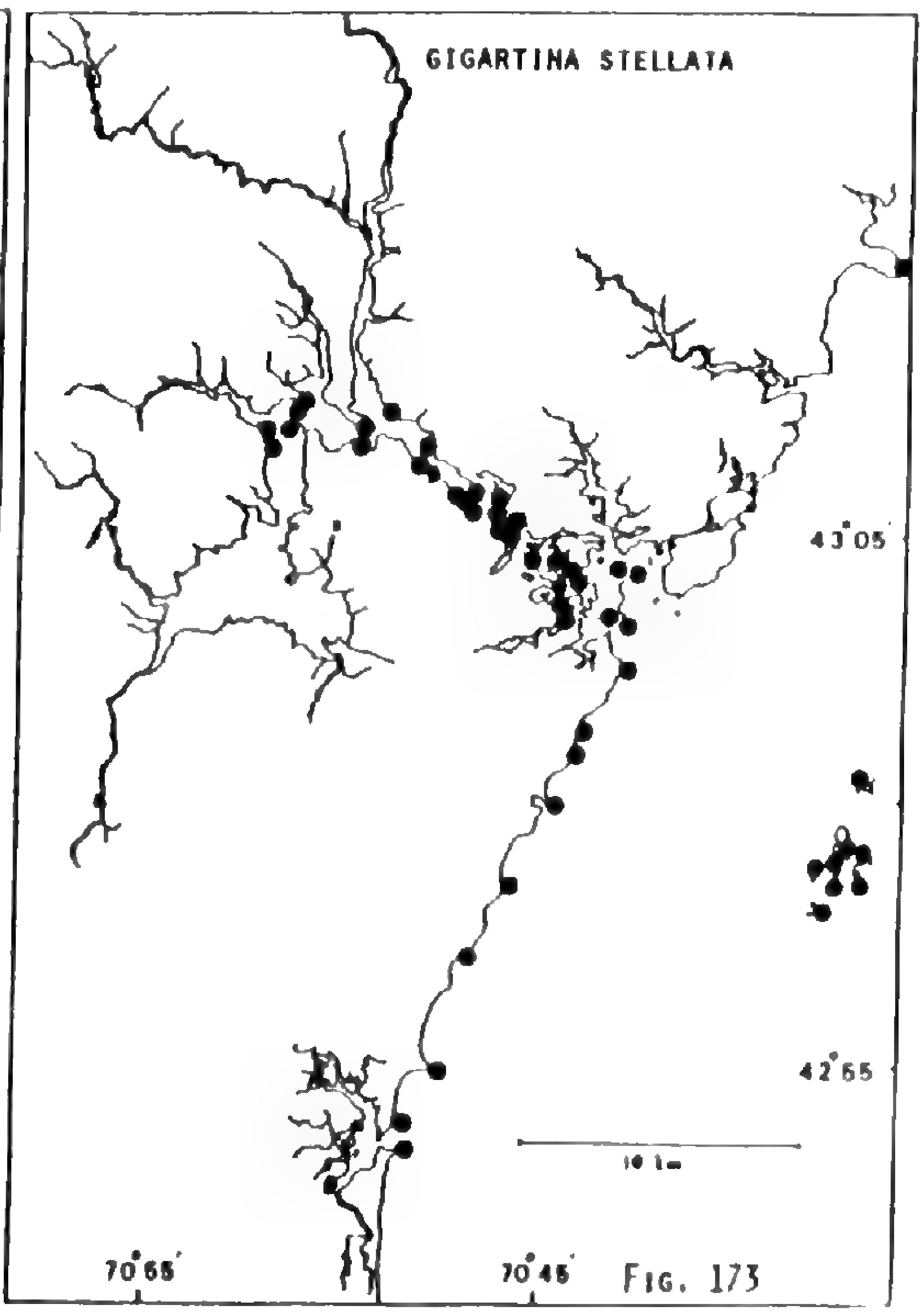


Fig. 173

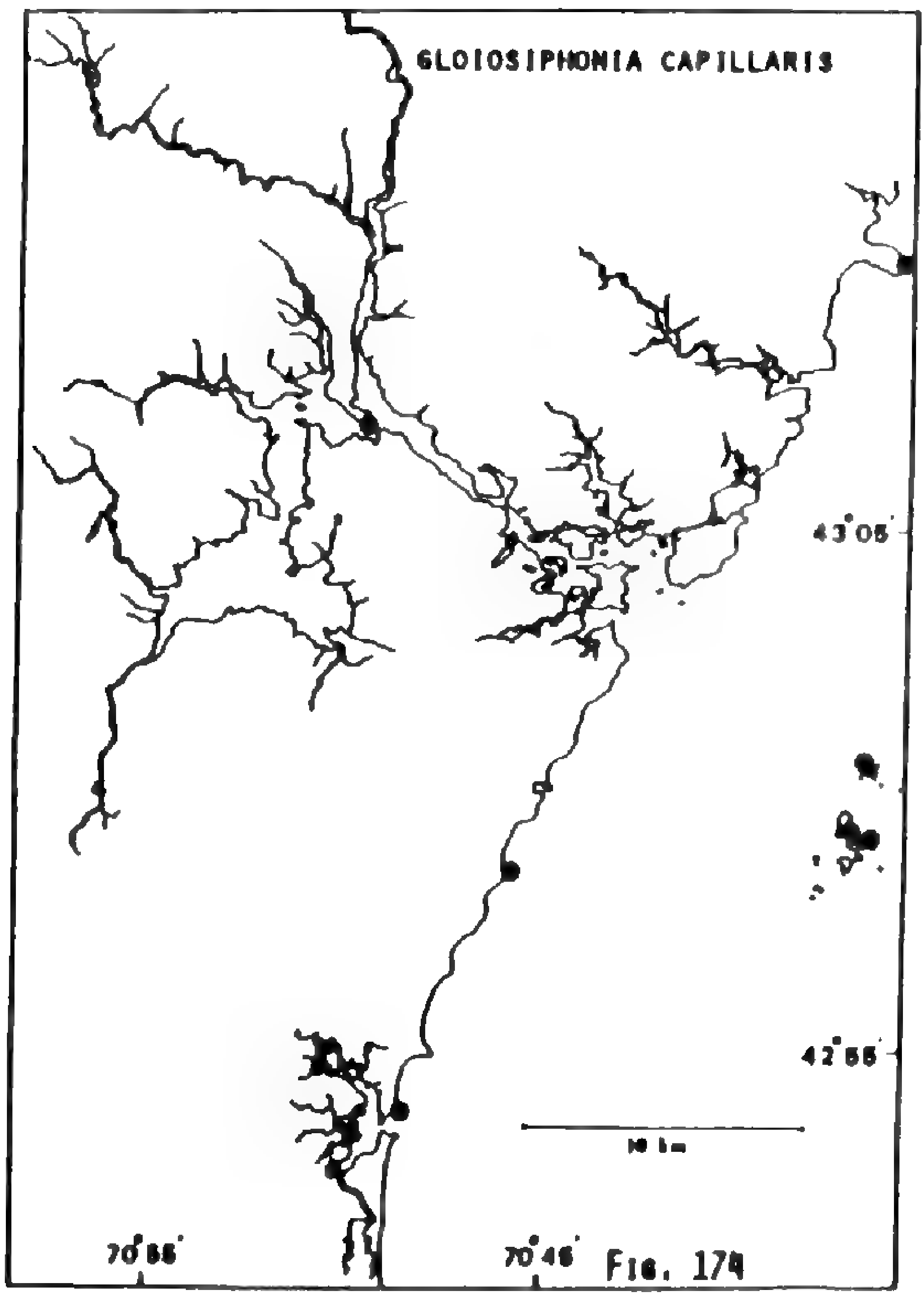


Fig. 174

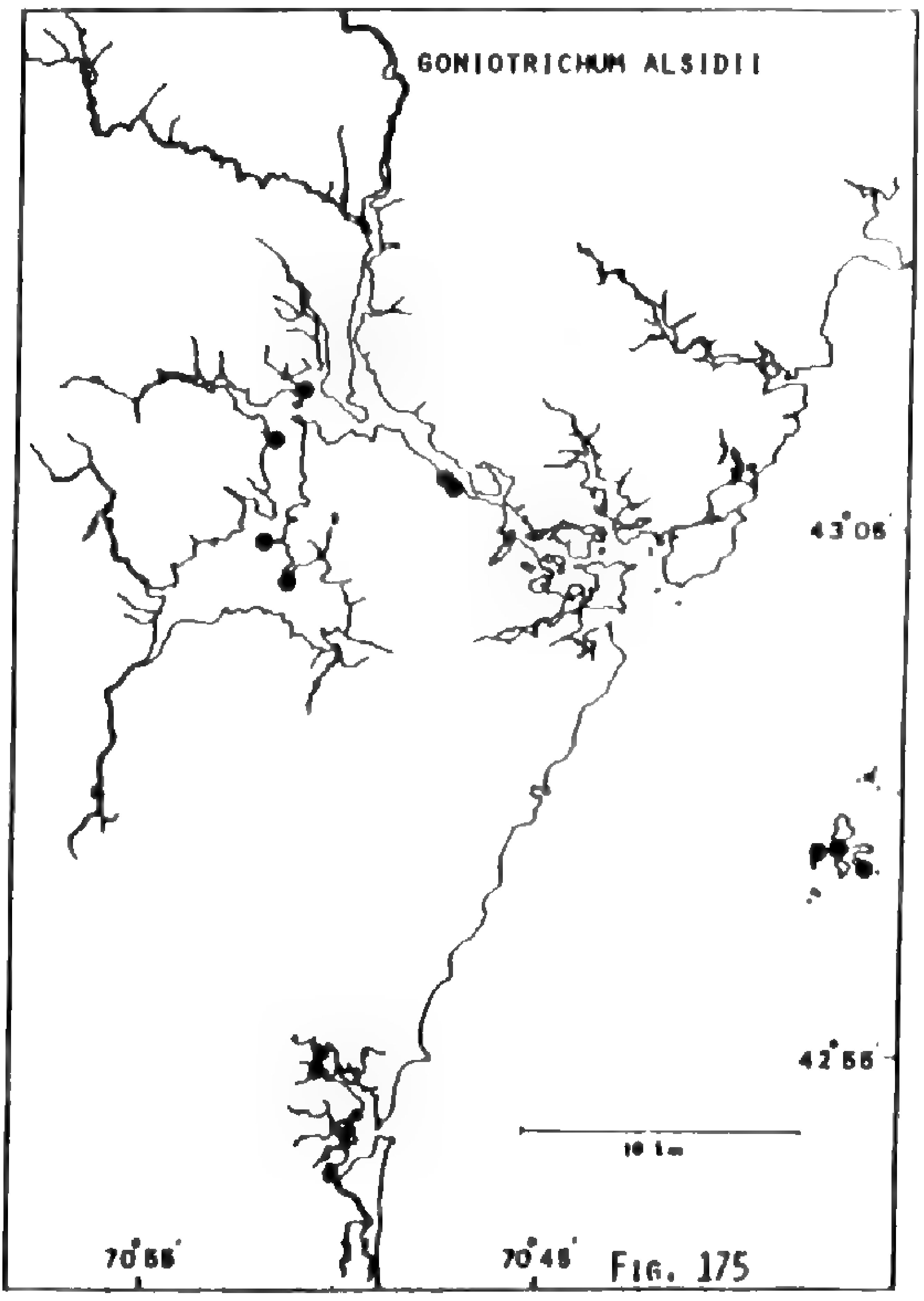


Fig. 175

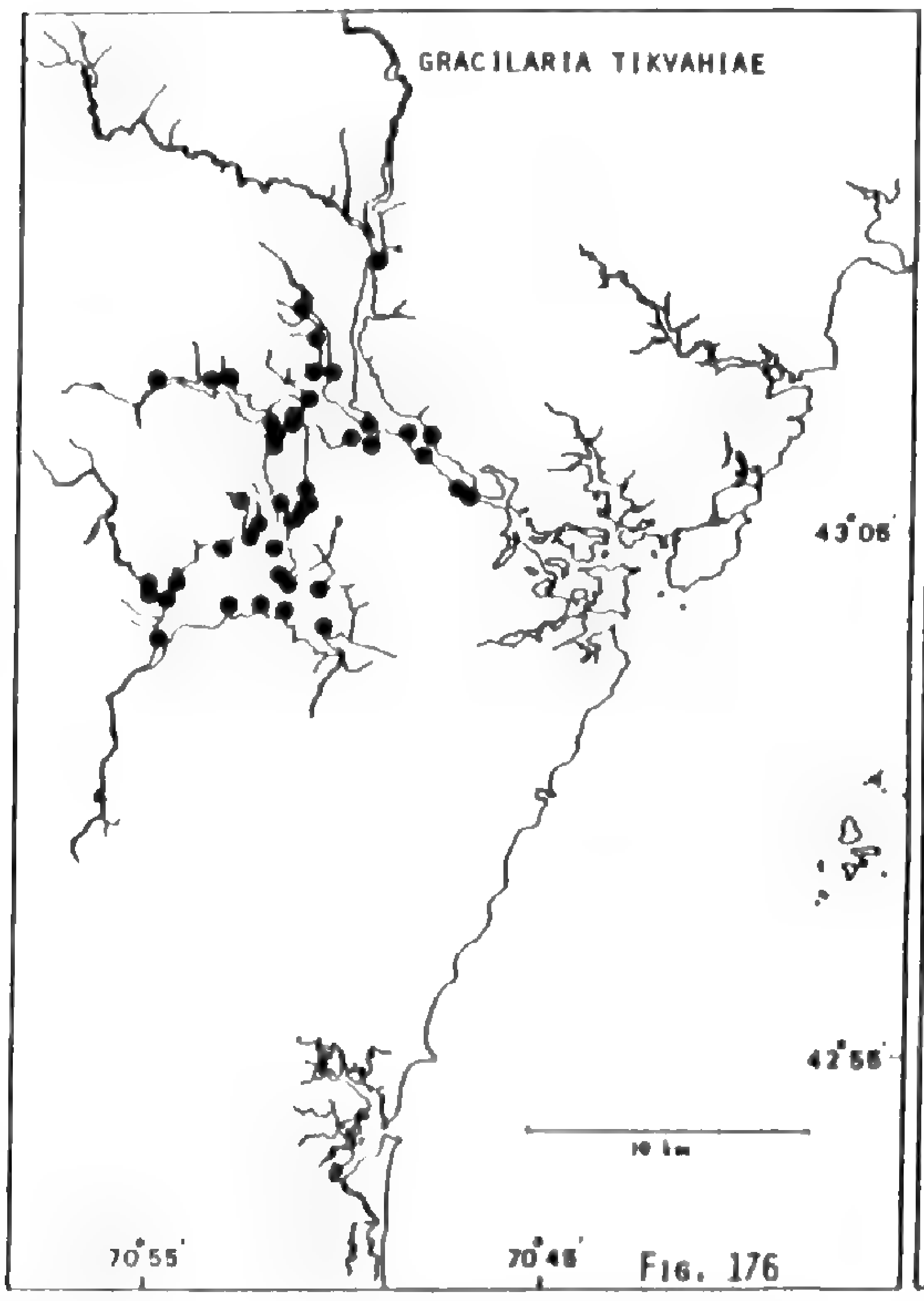


Fig. 176

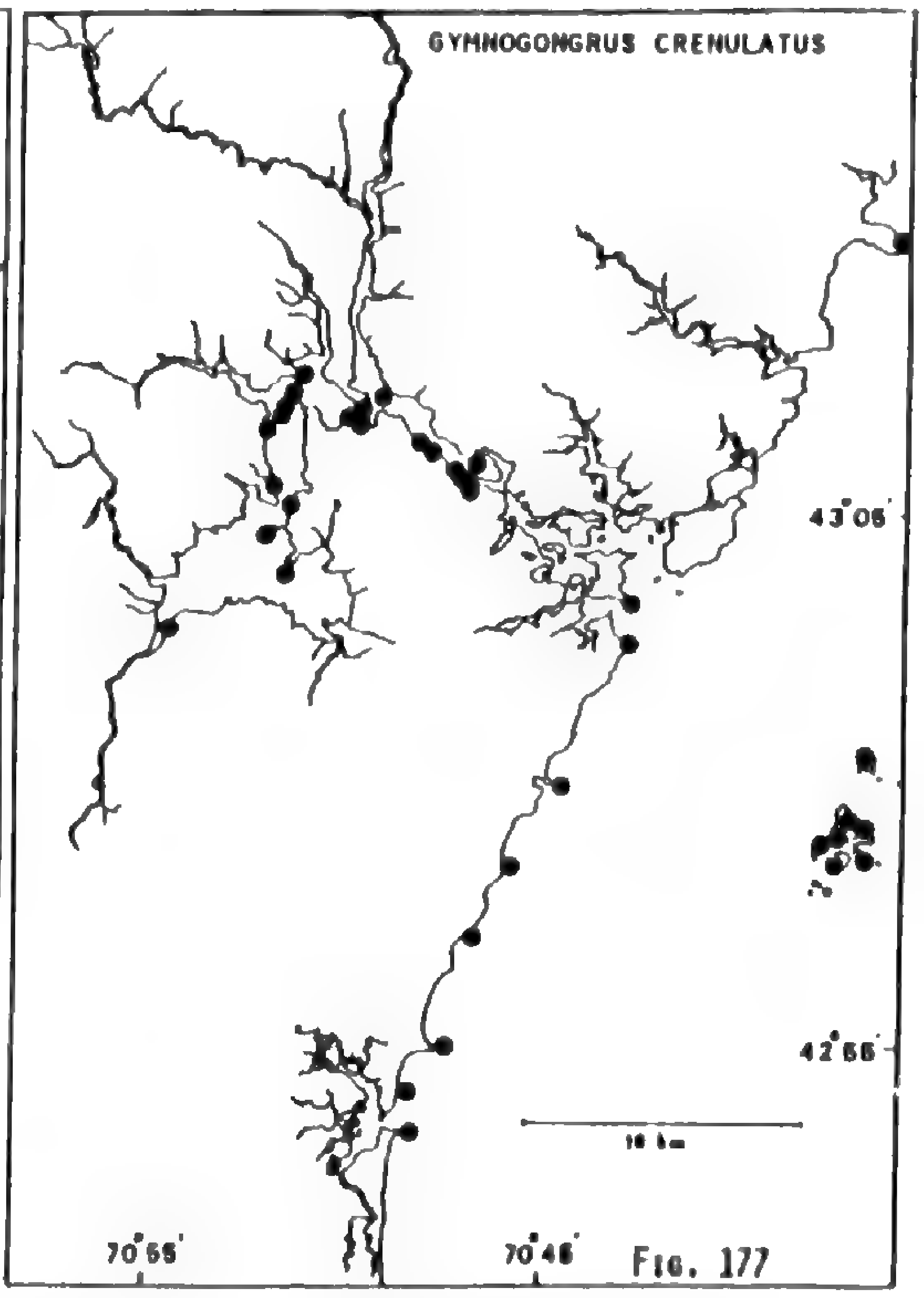


Fig. 177

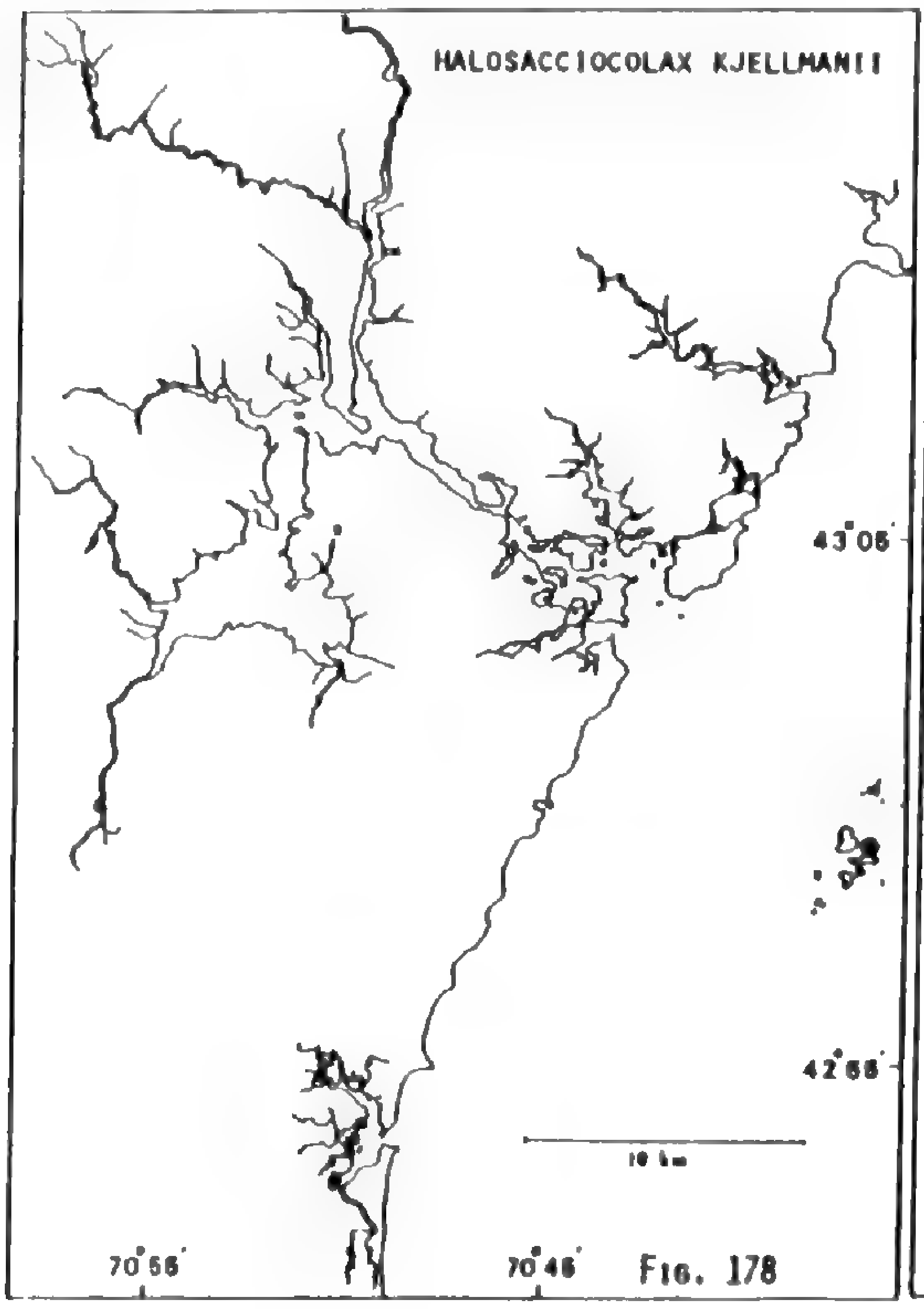
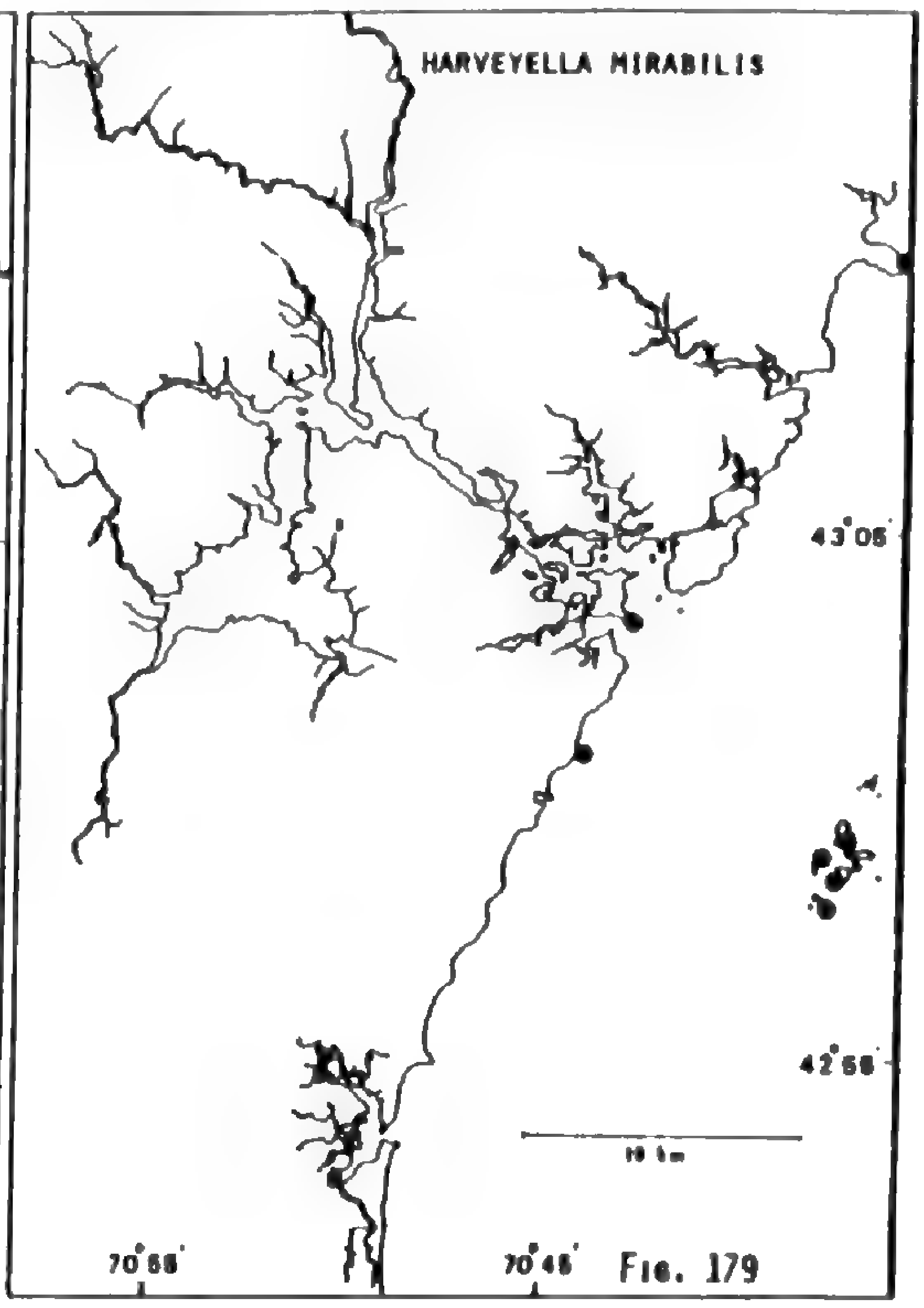


Fig. 178



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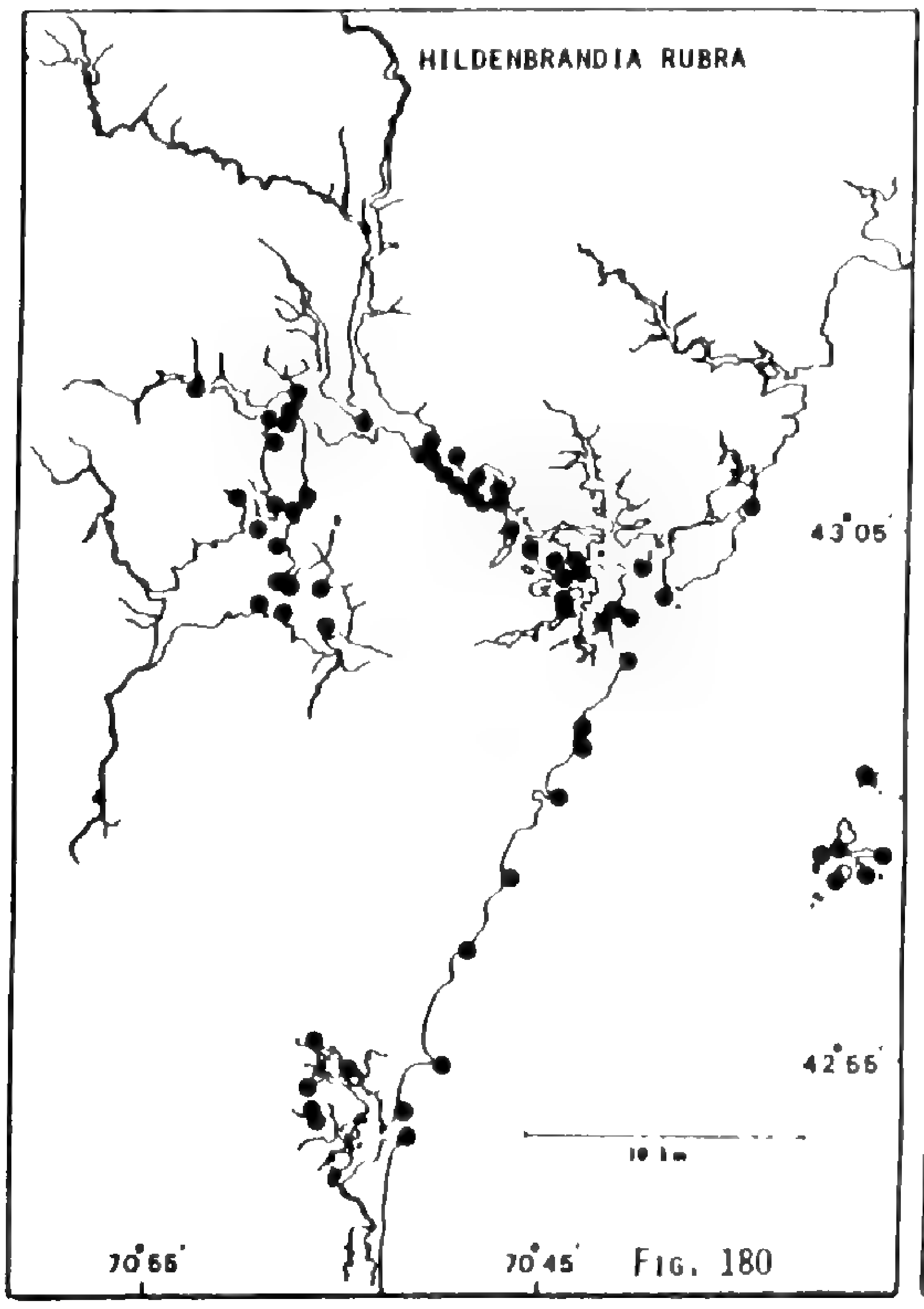

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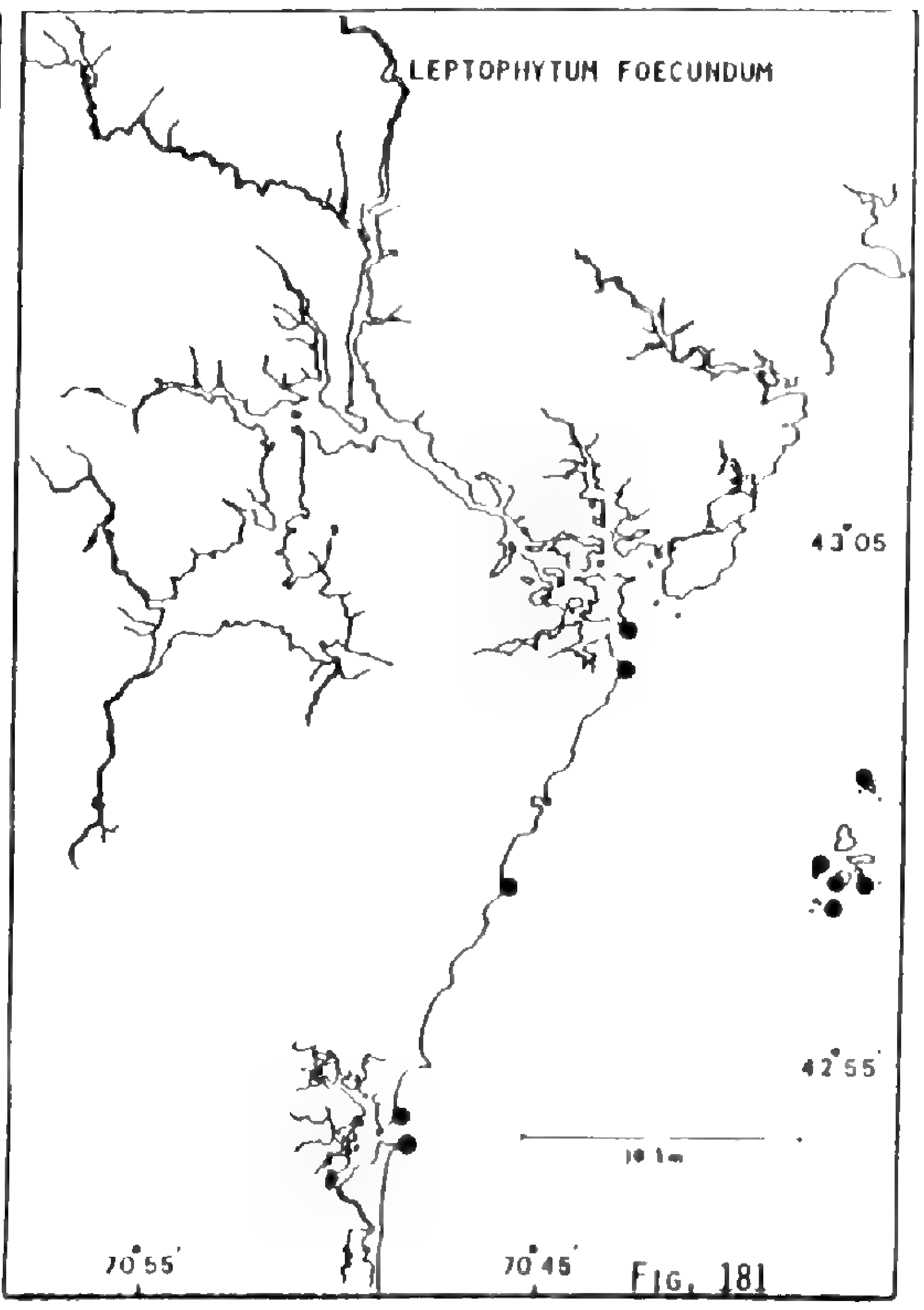

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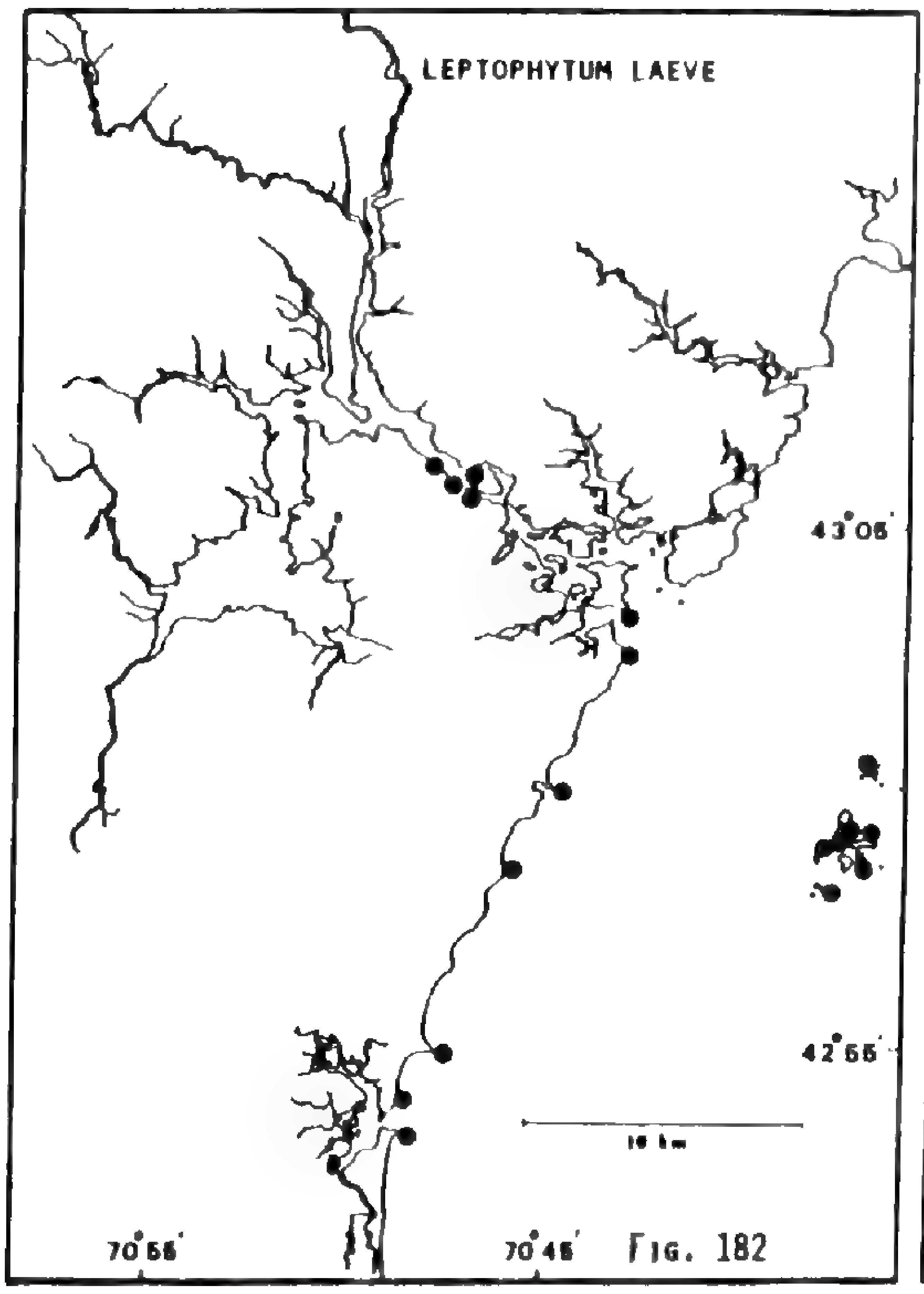

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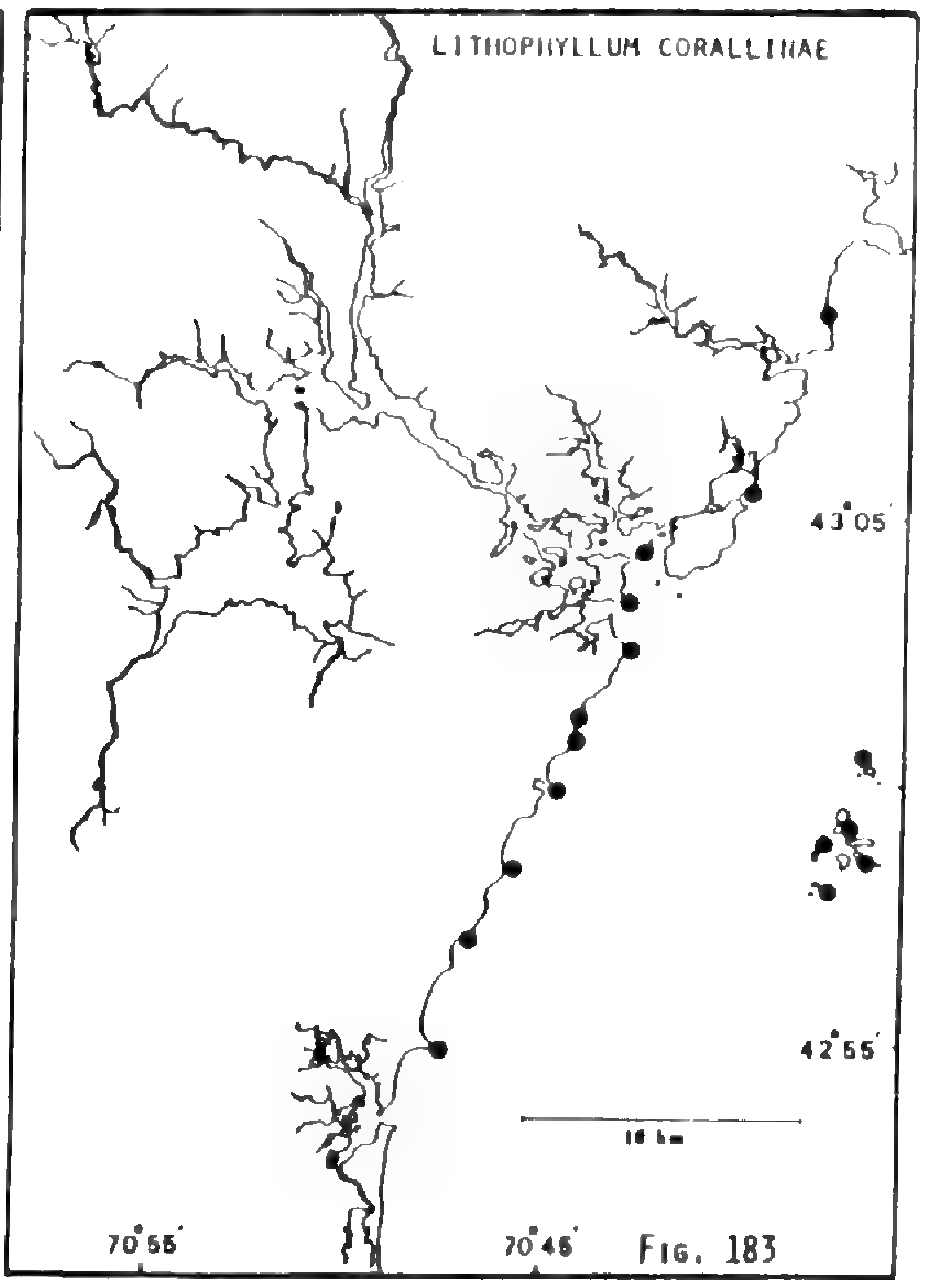

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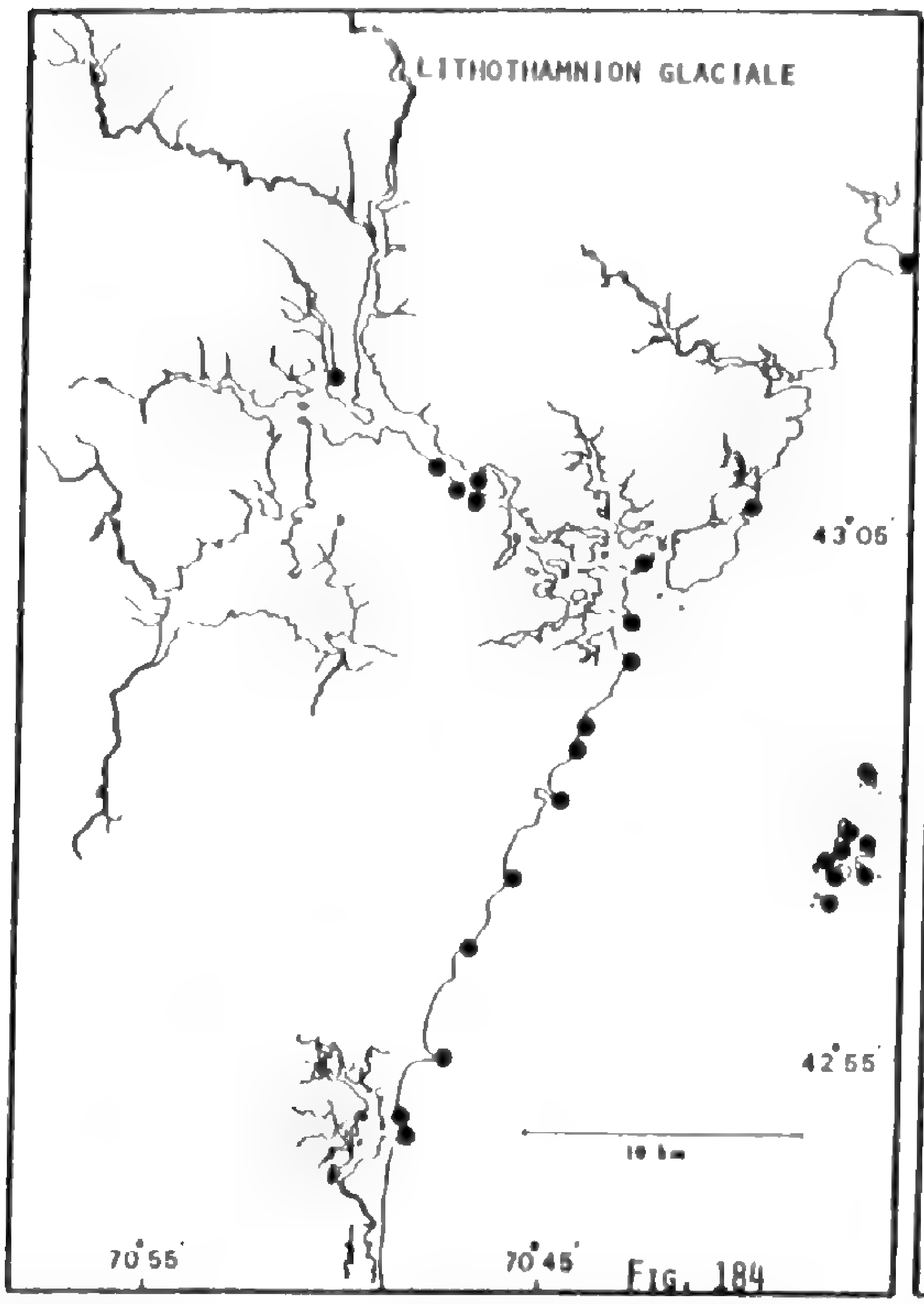

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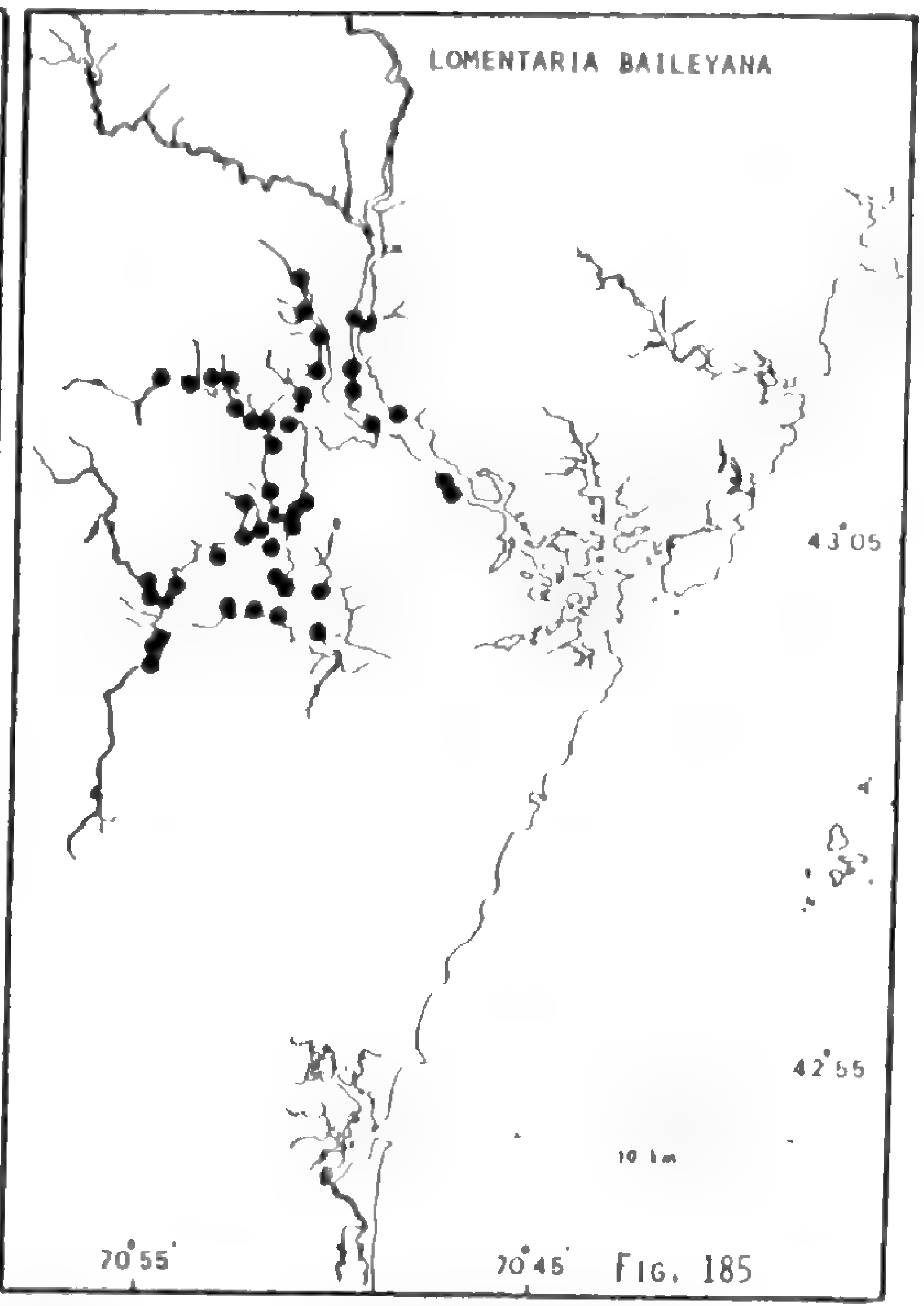

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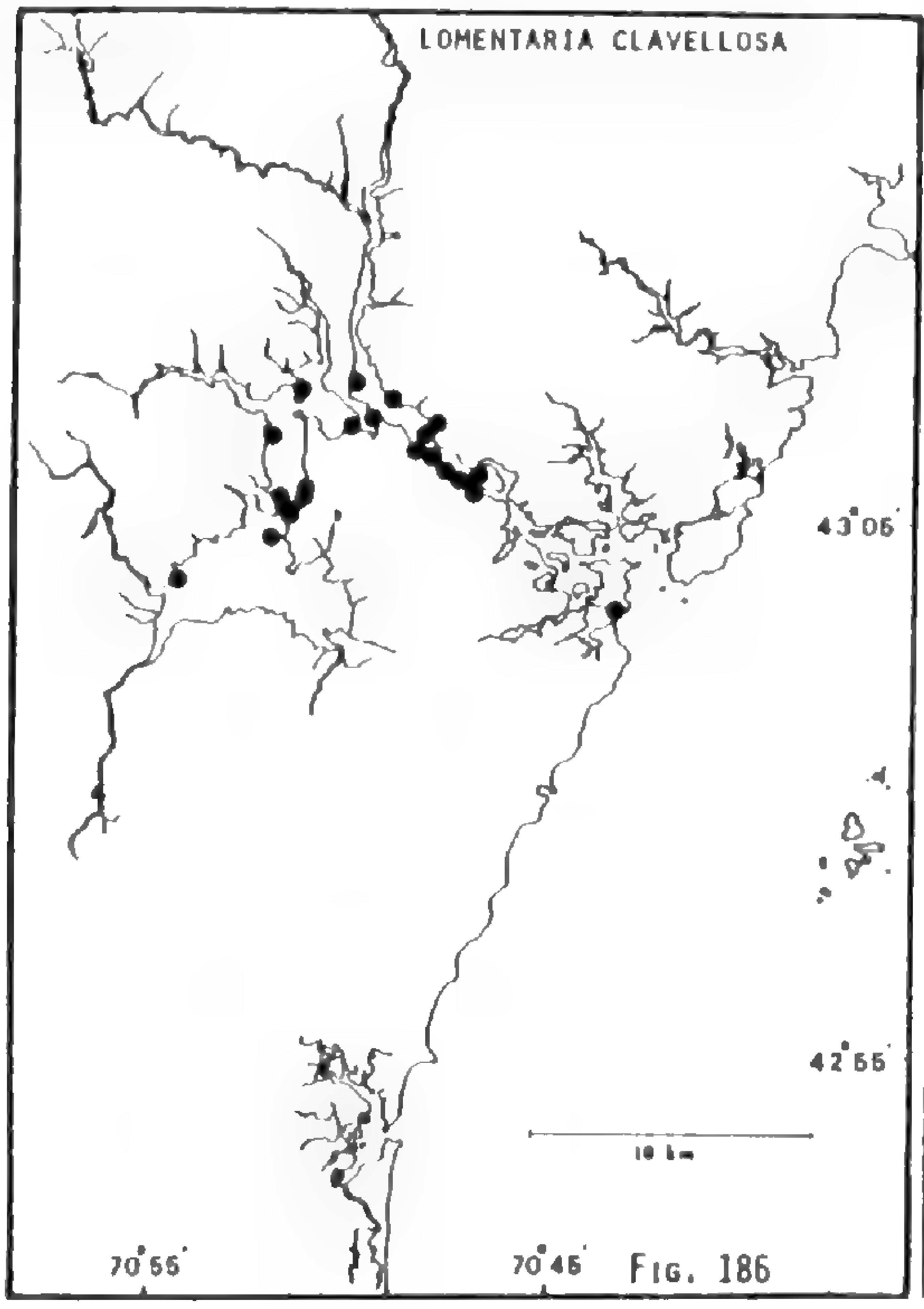

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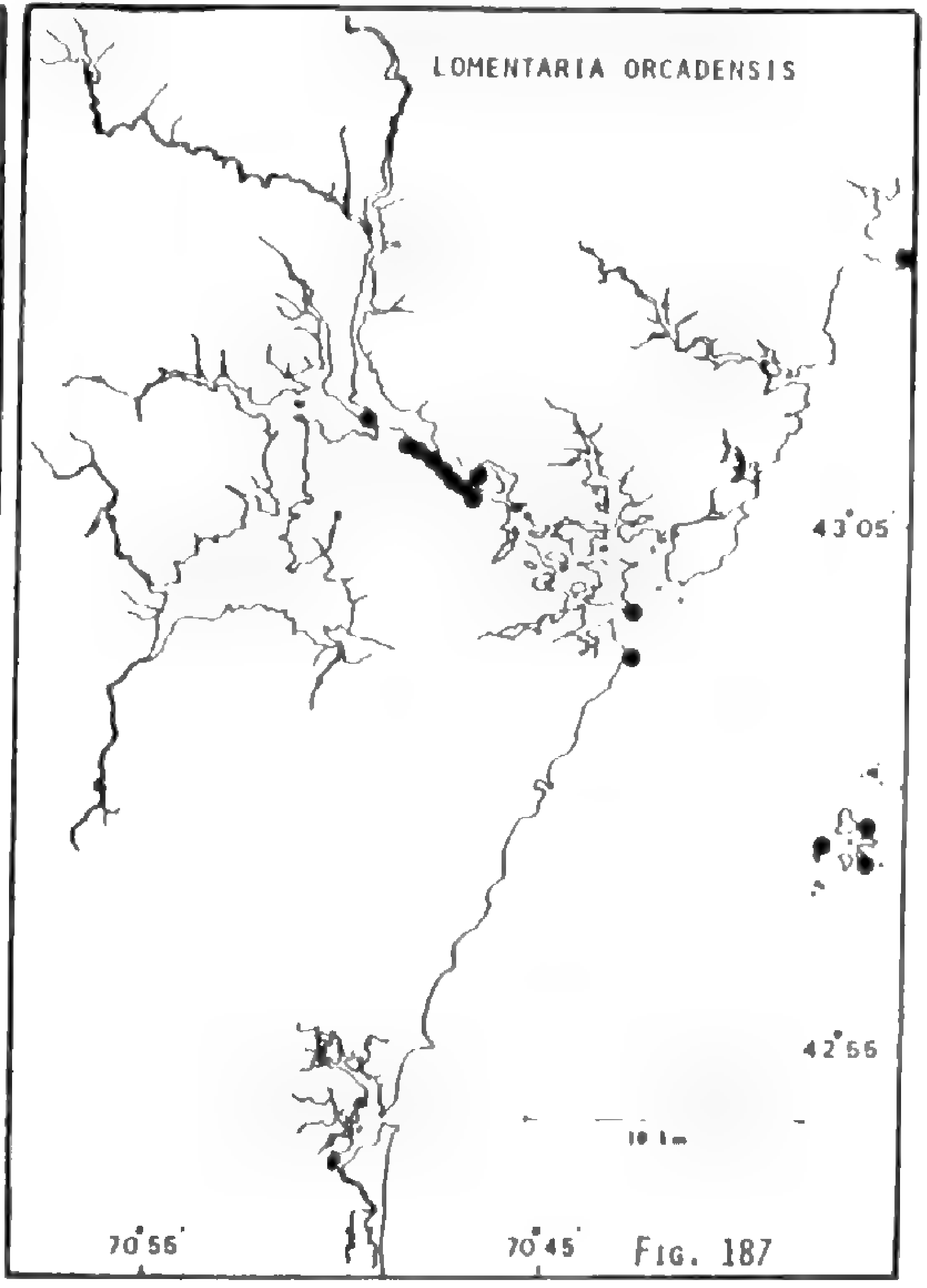

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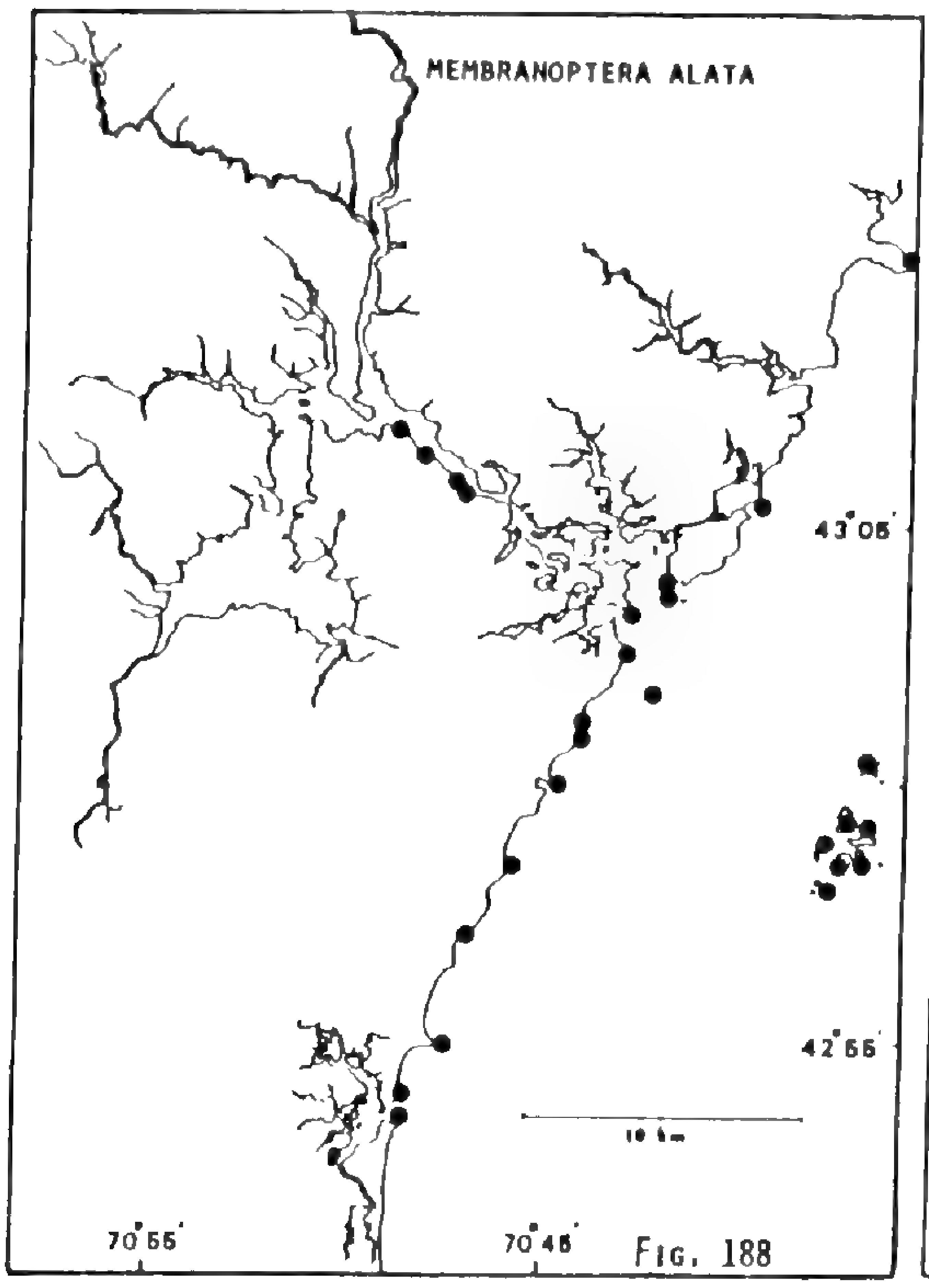

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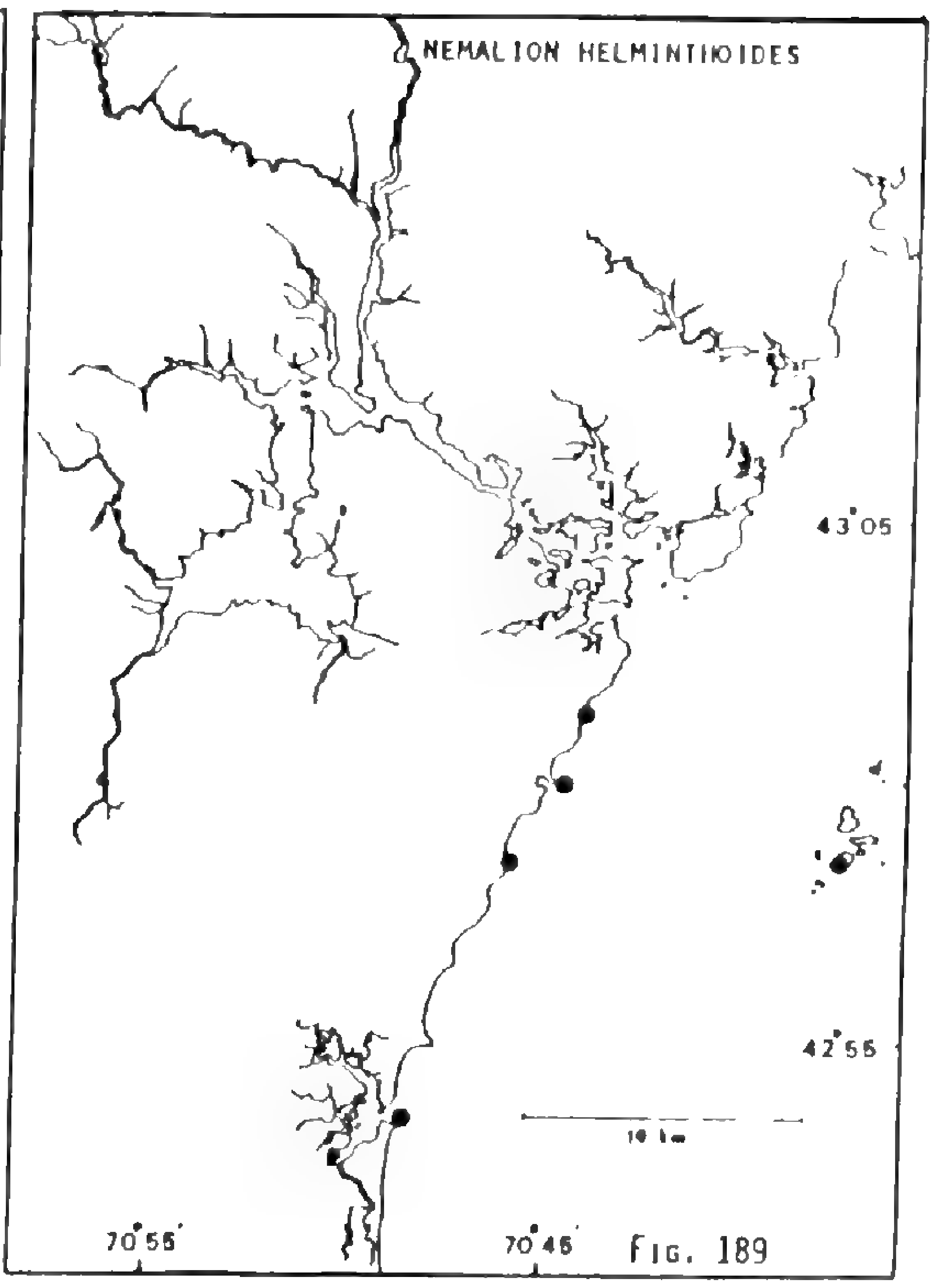

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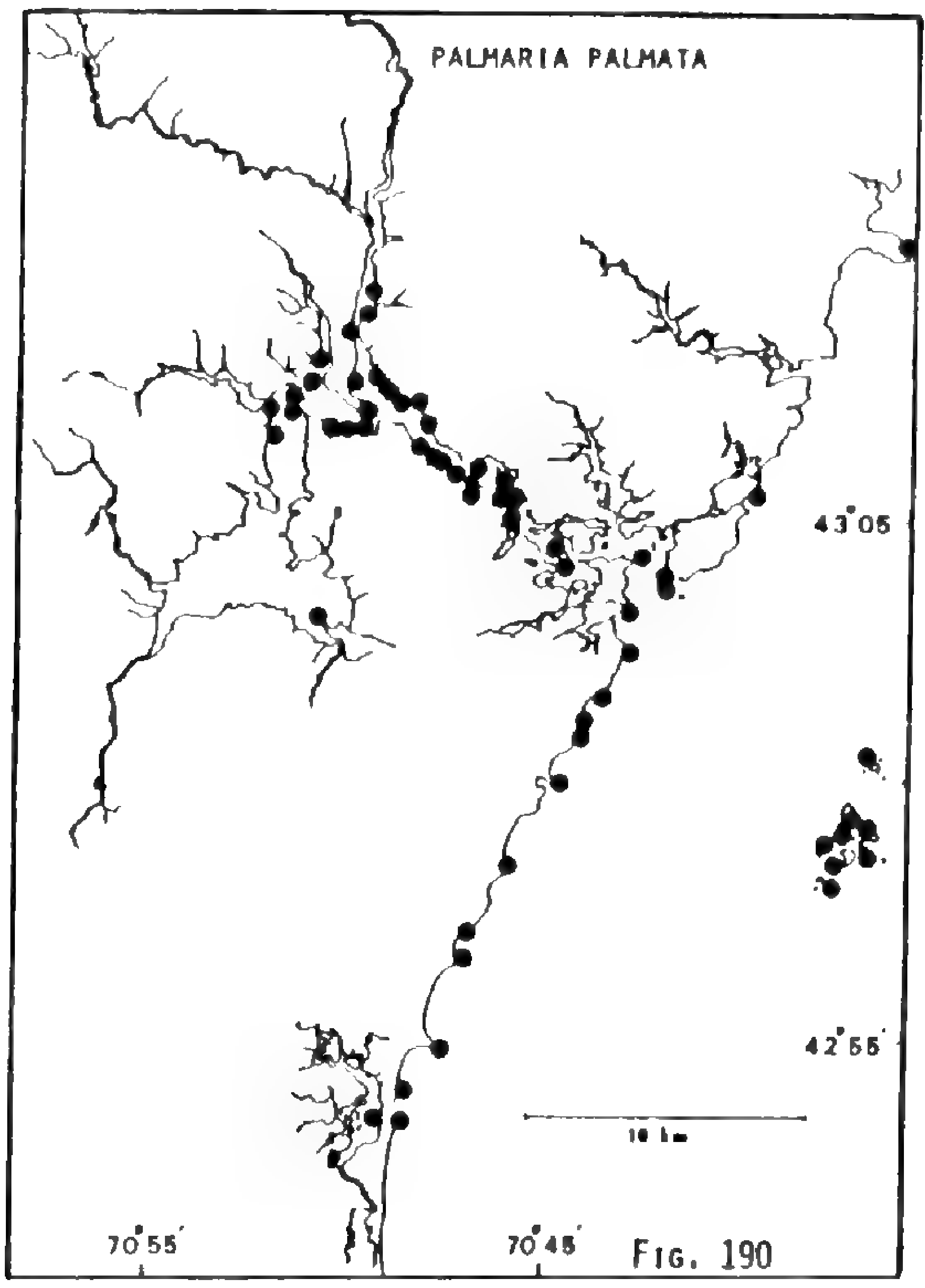

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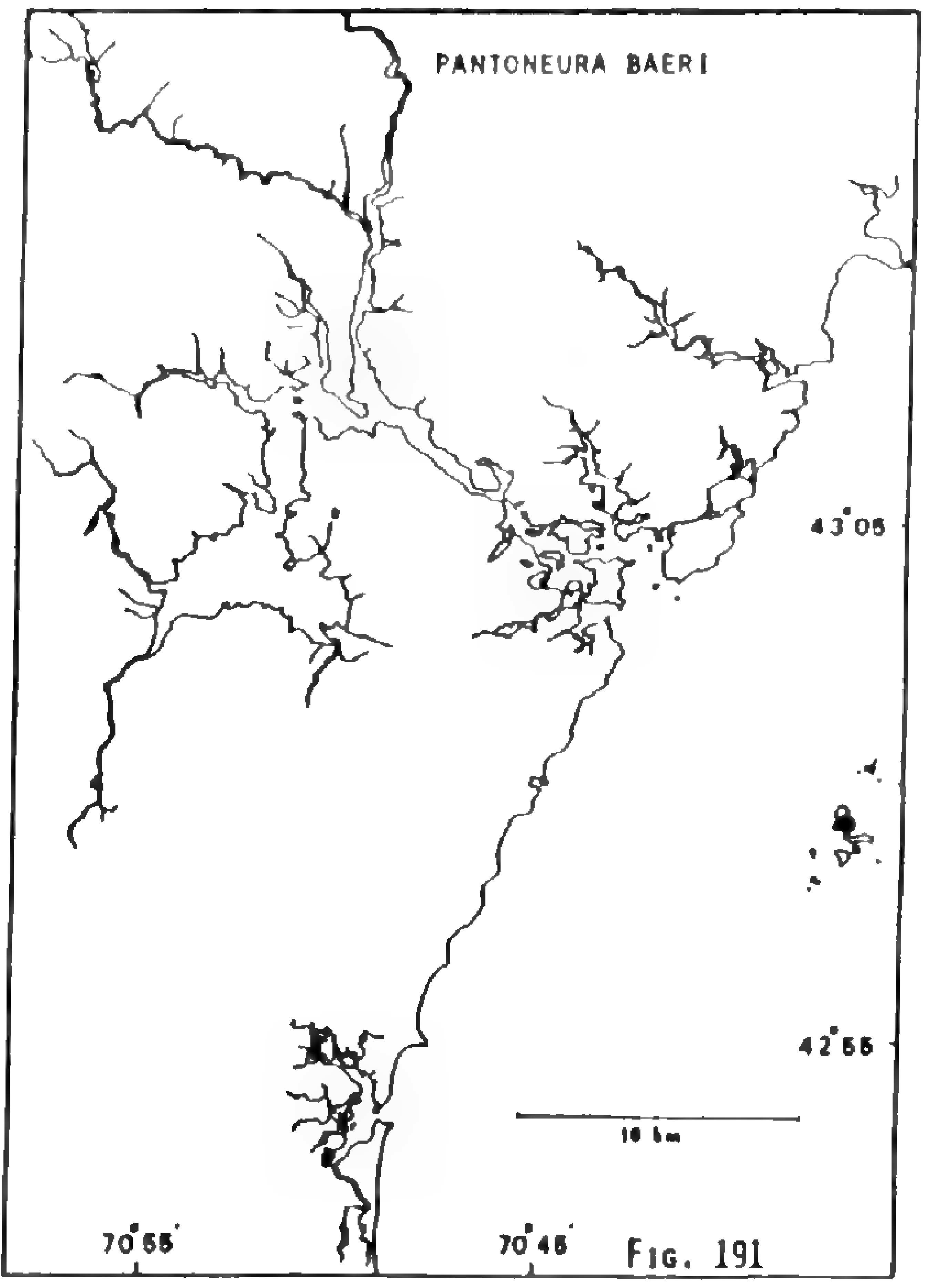

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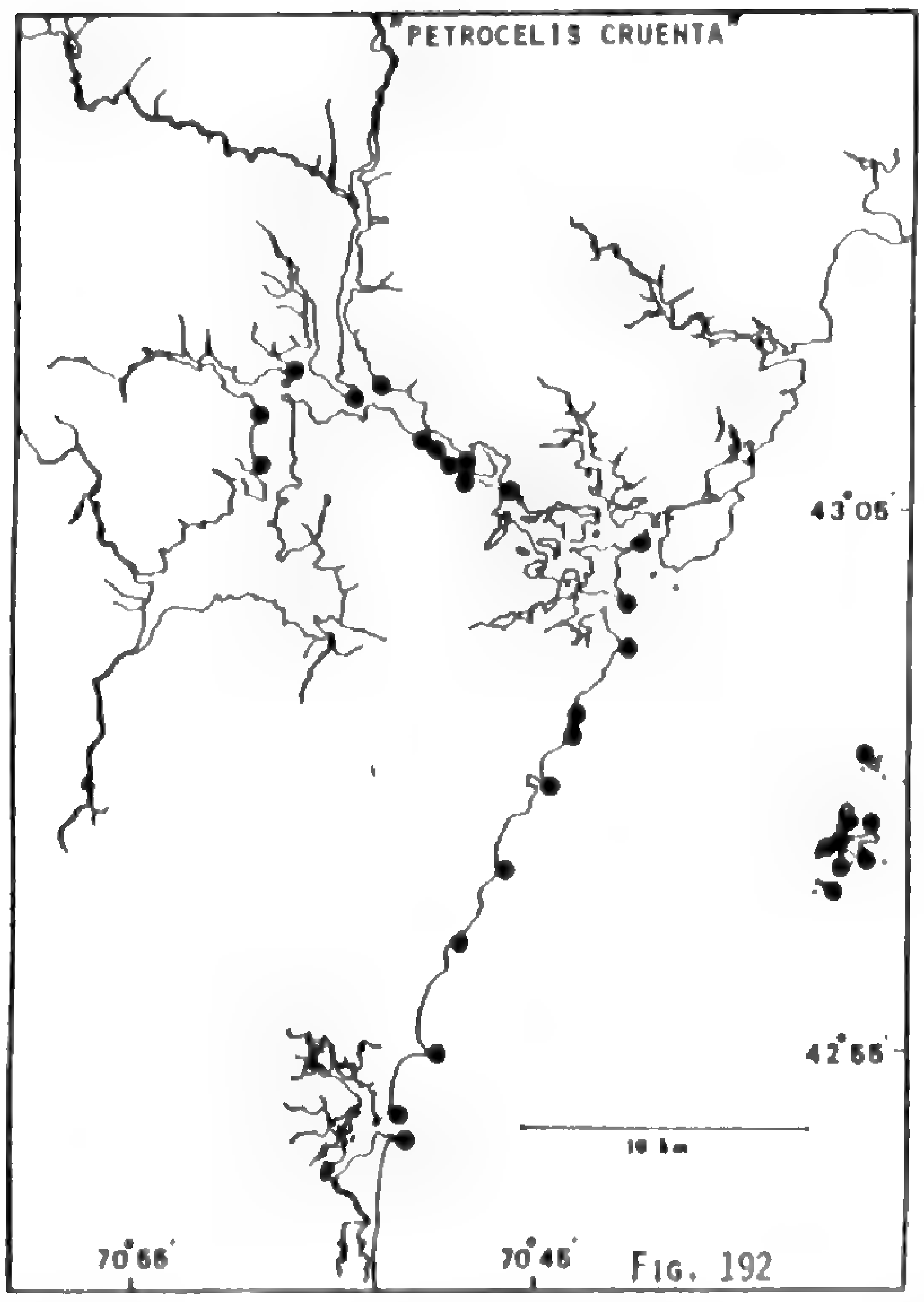


FIG. 192

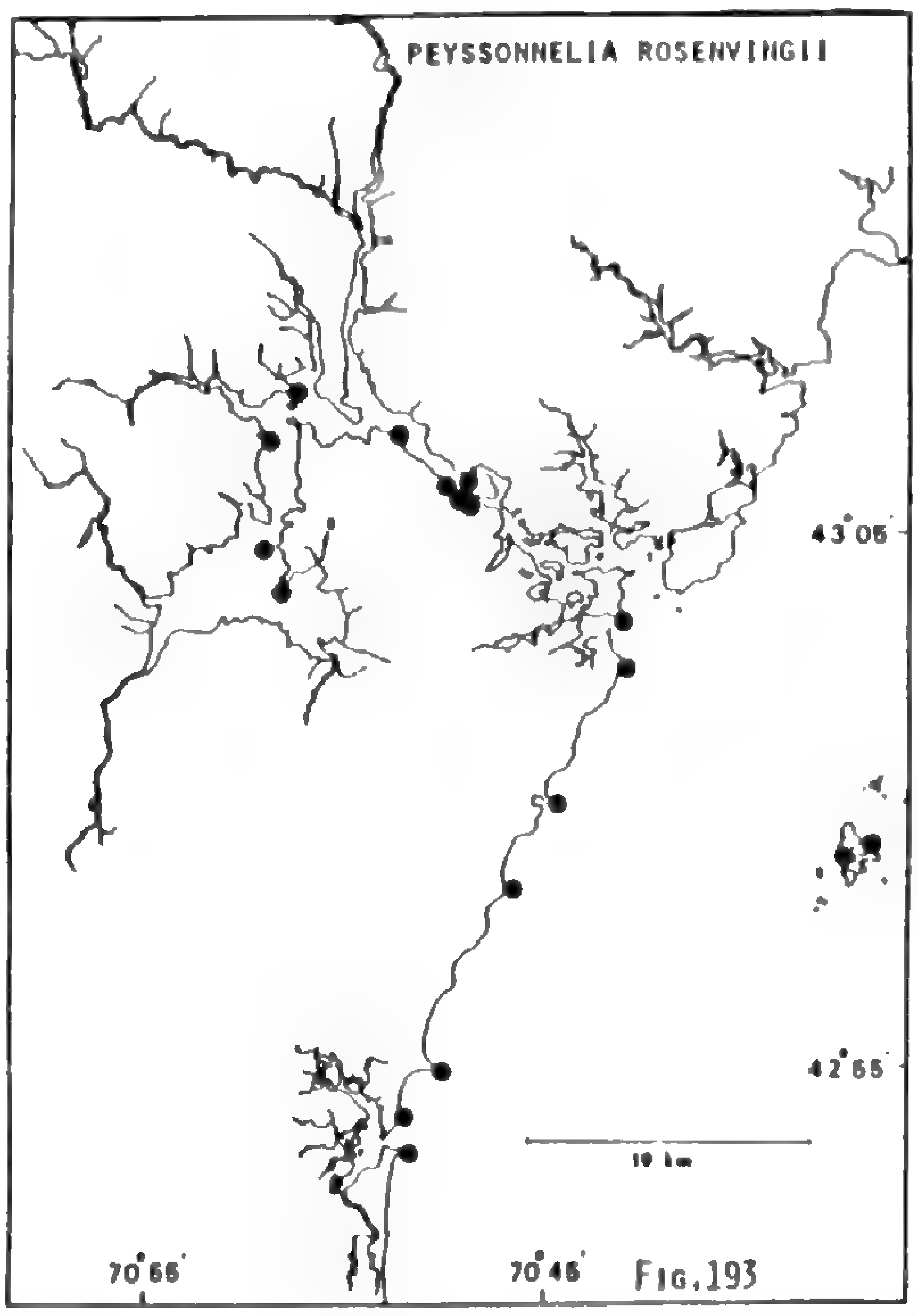


FIG. 193

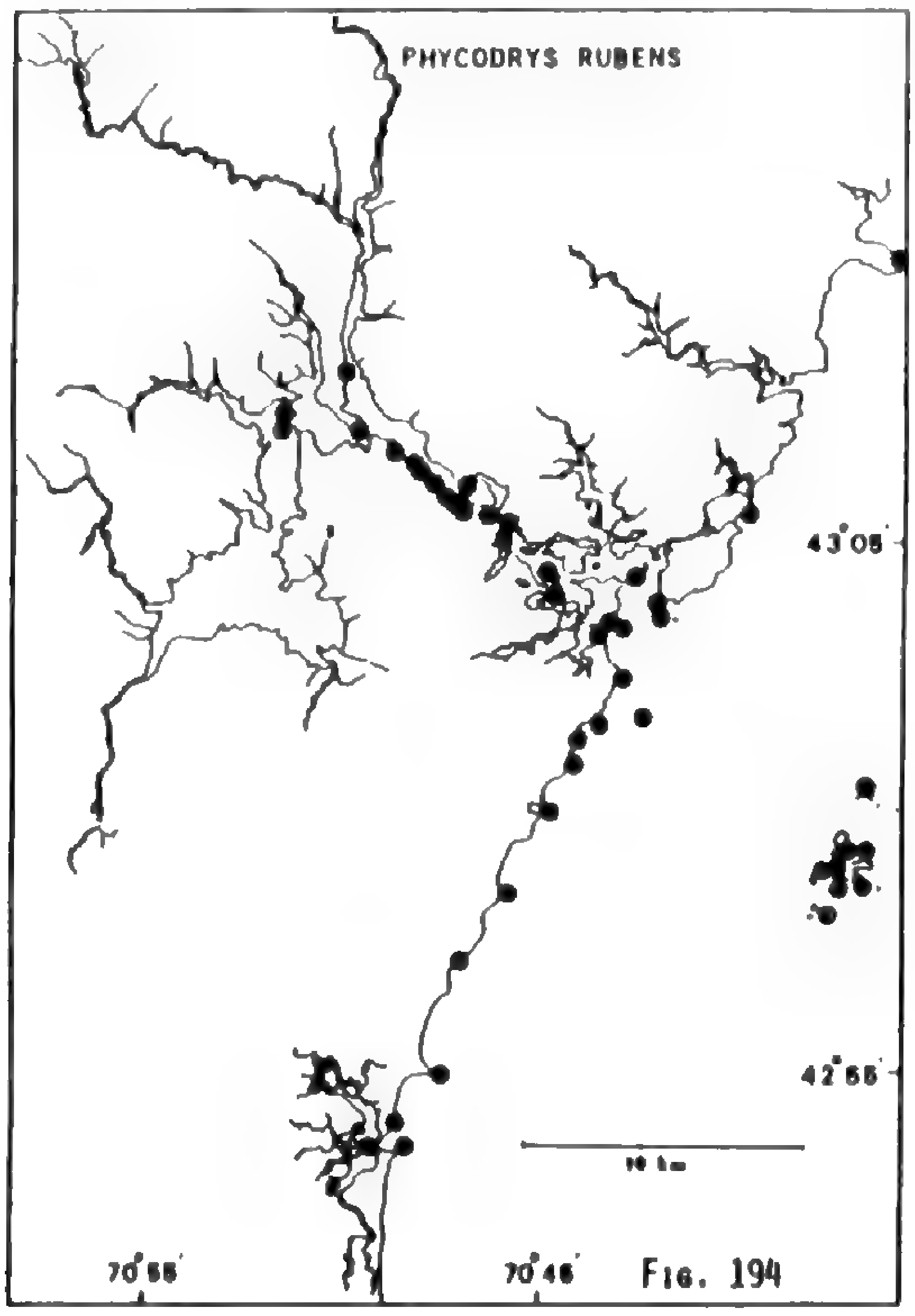


FIG. 194

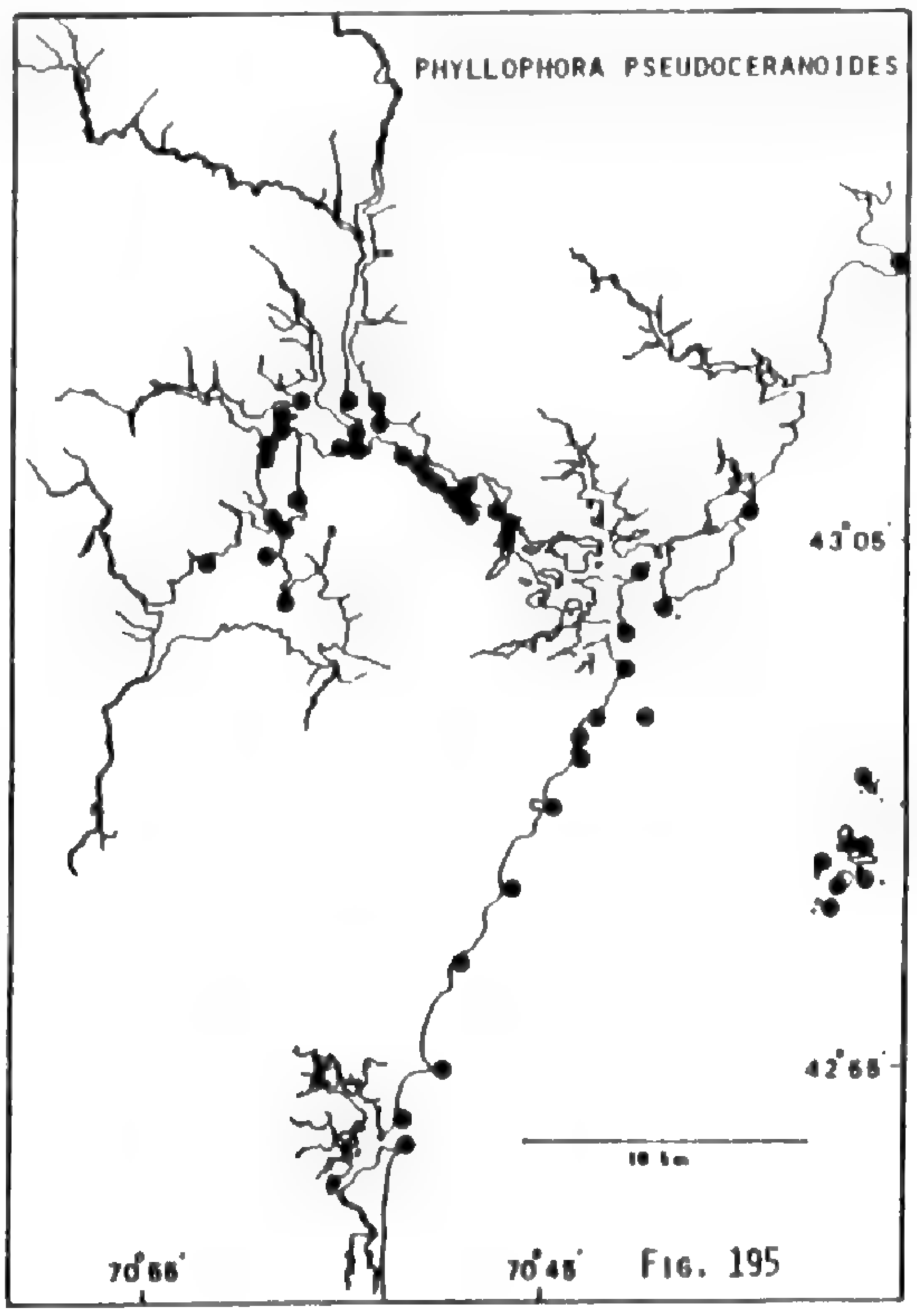
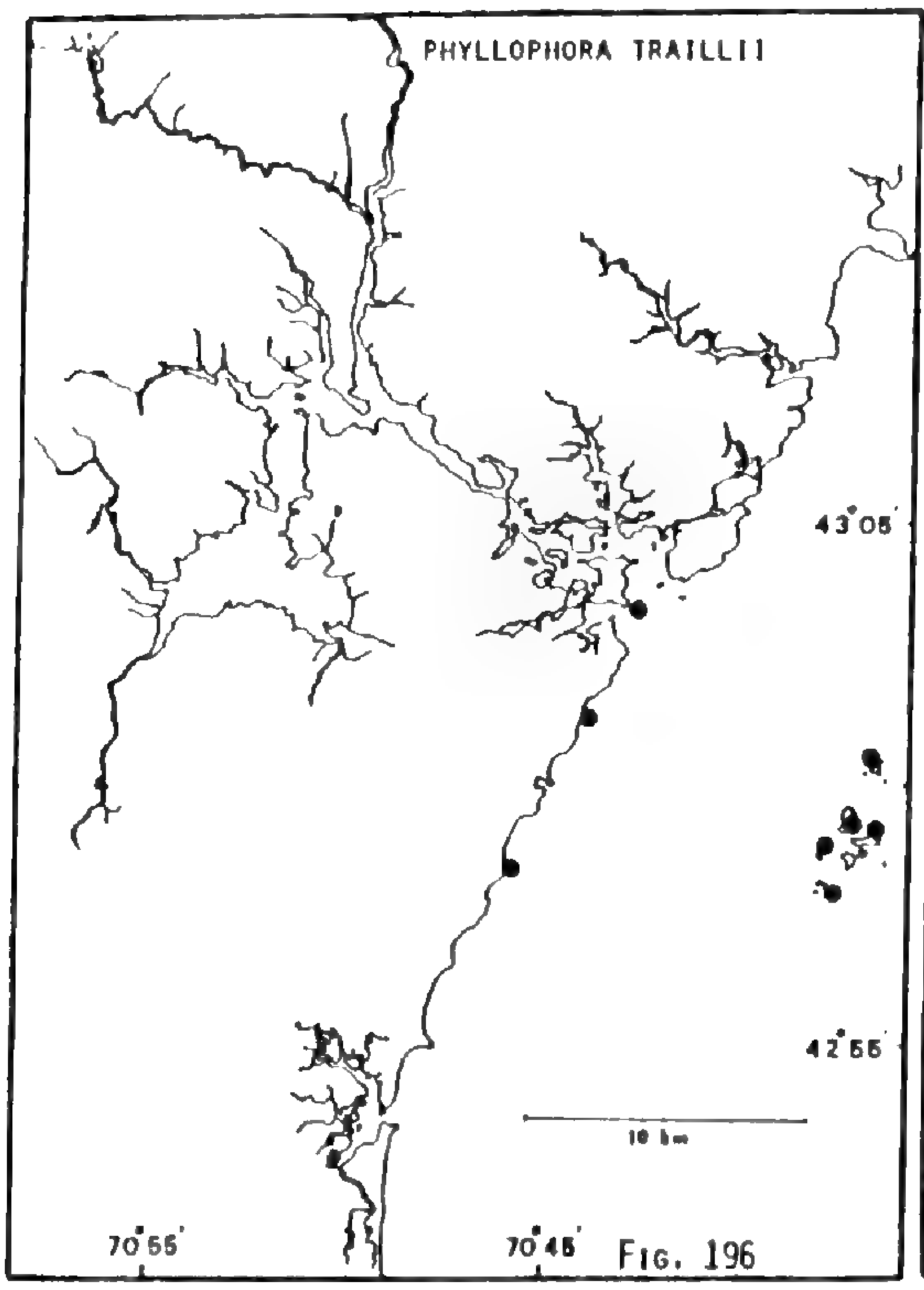


FIG. 195



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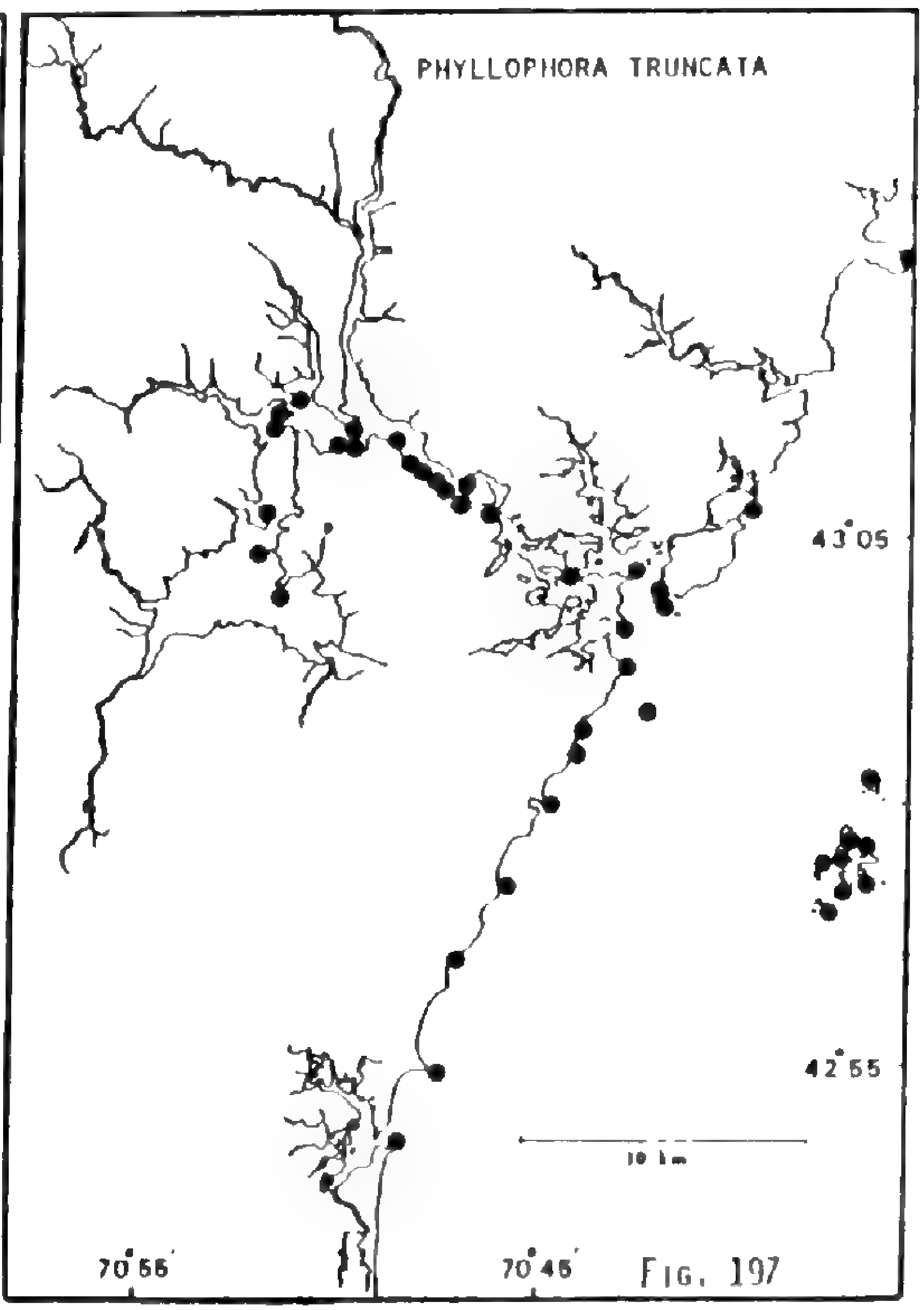

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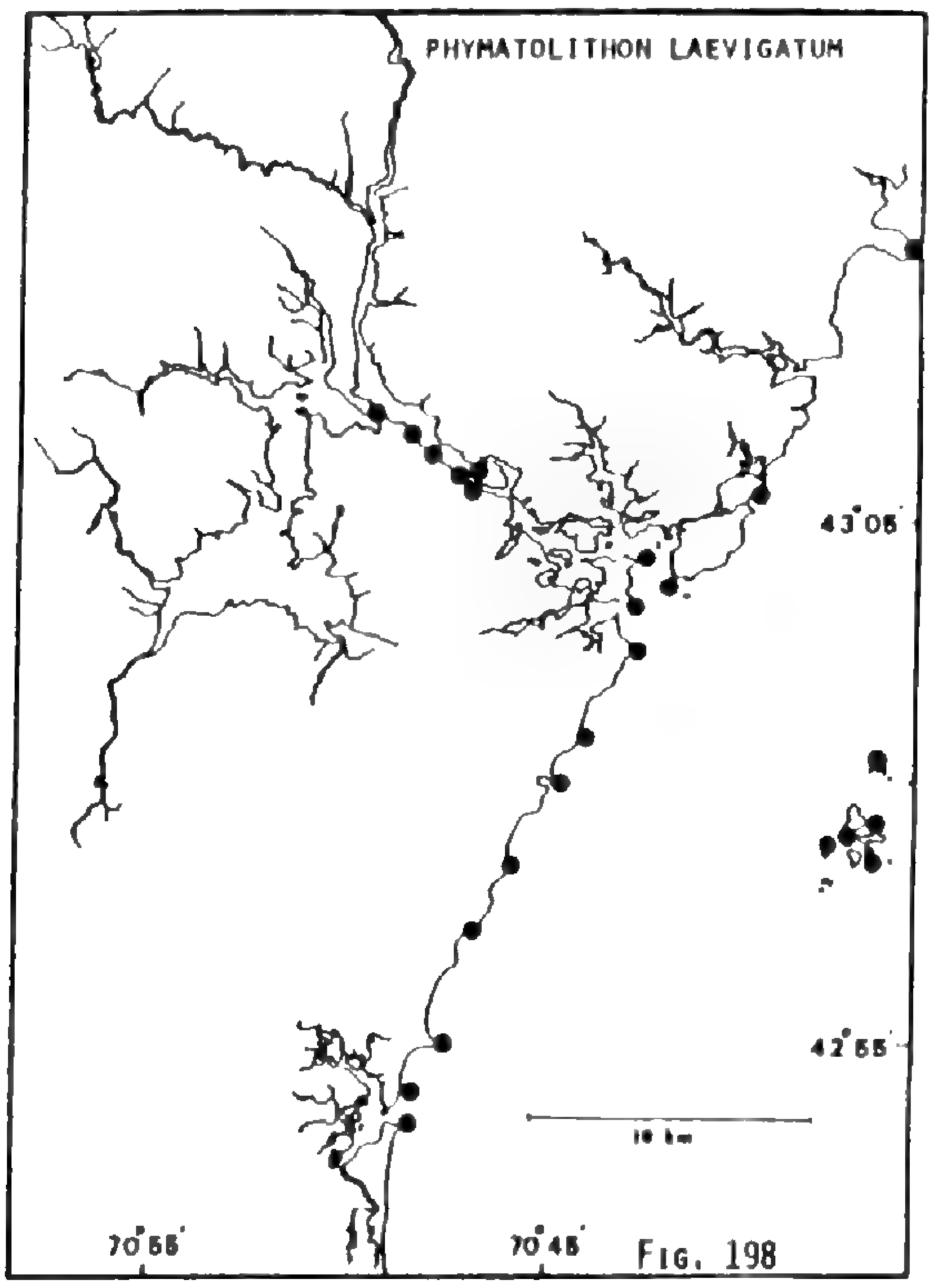

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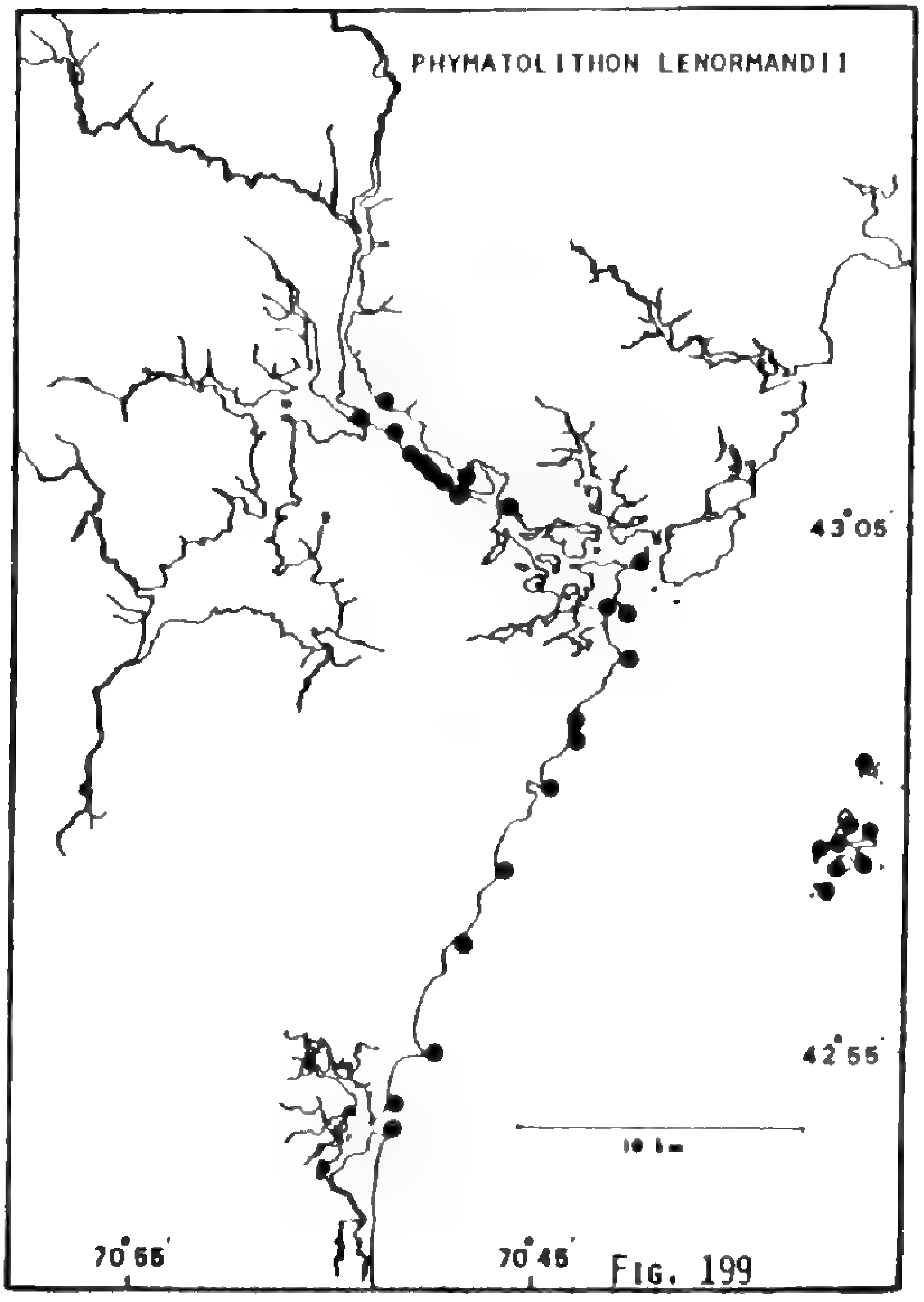

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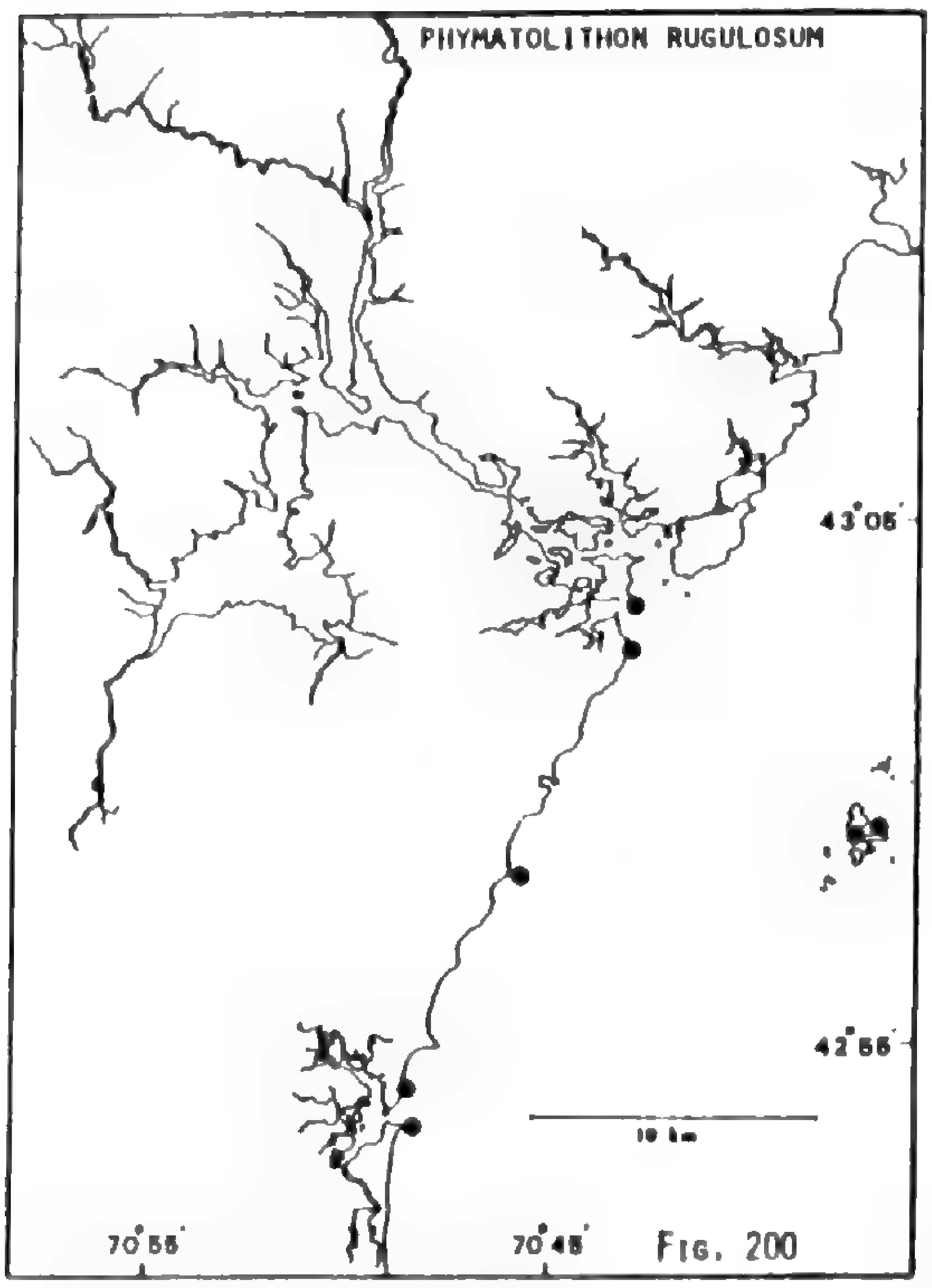

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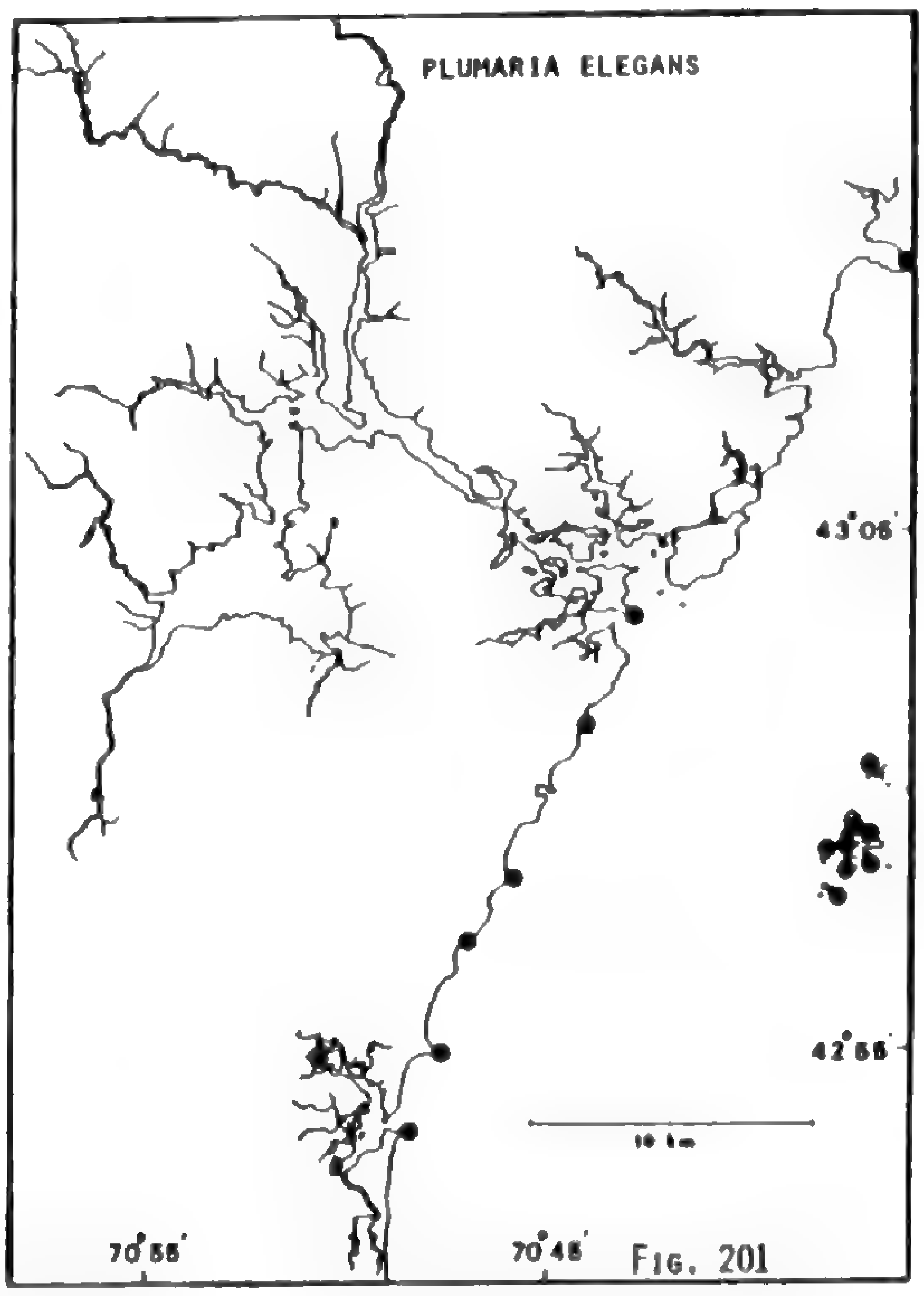
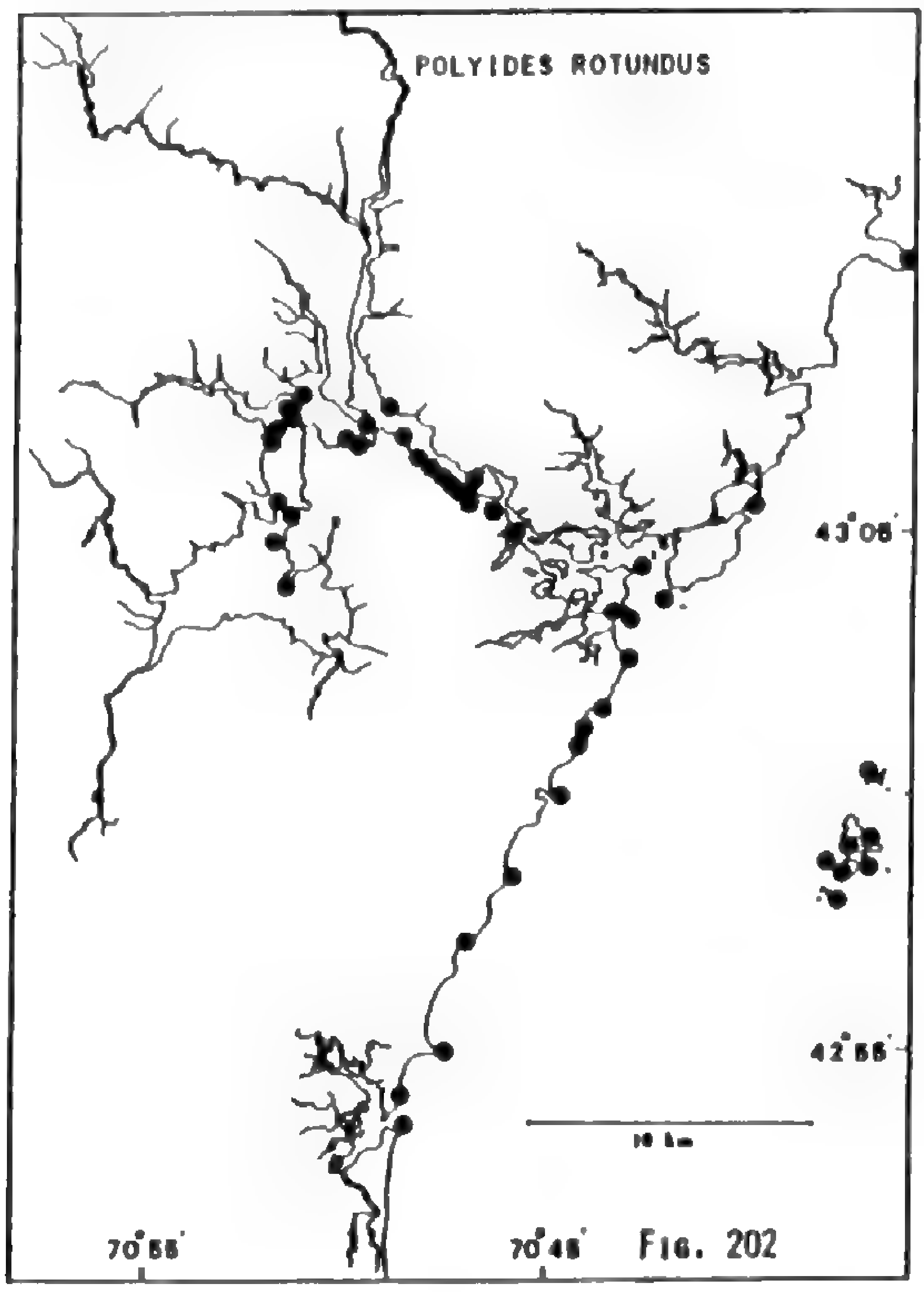


Fig. 201



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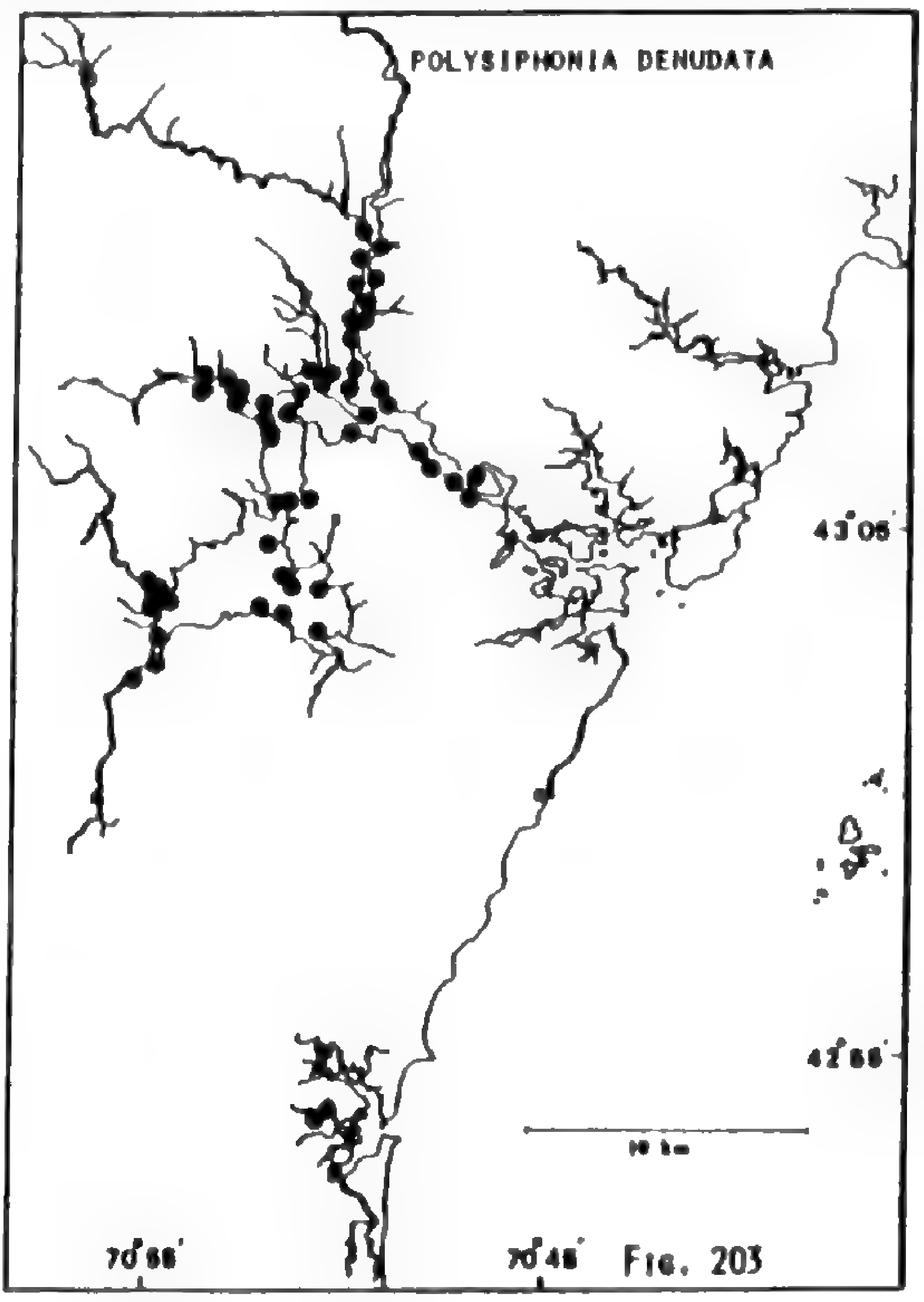


Fig. 203

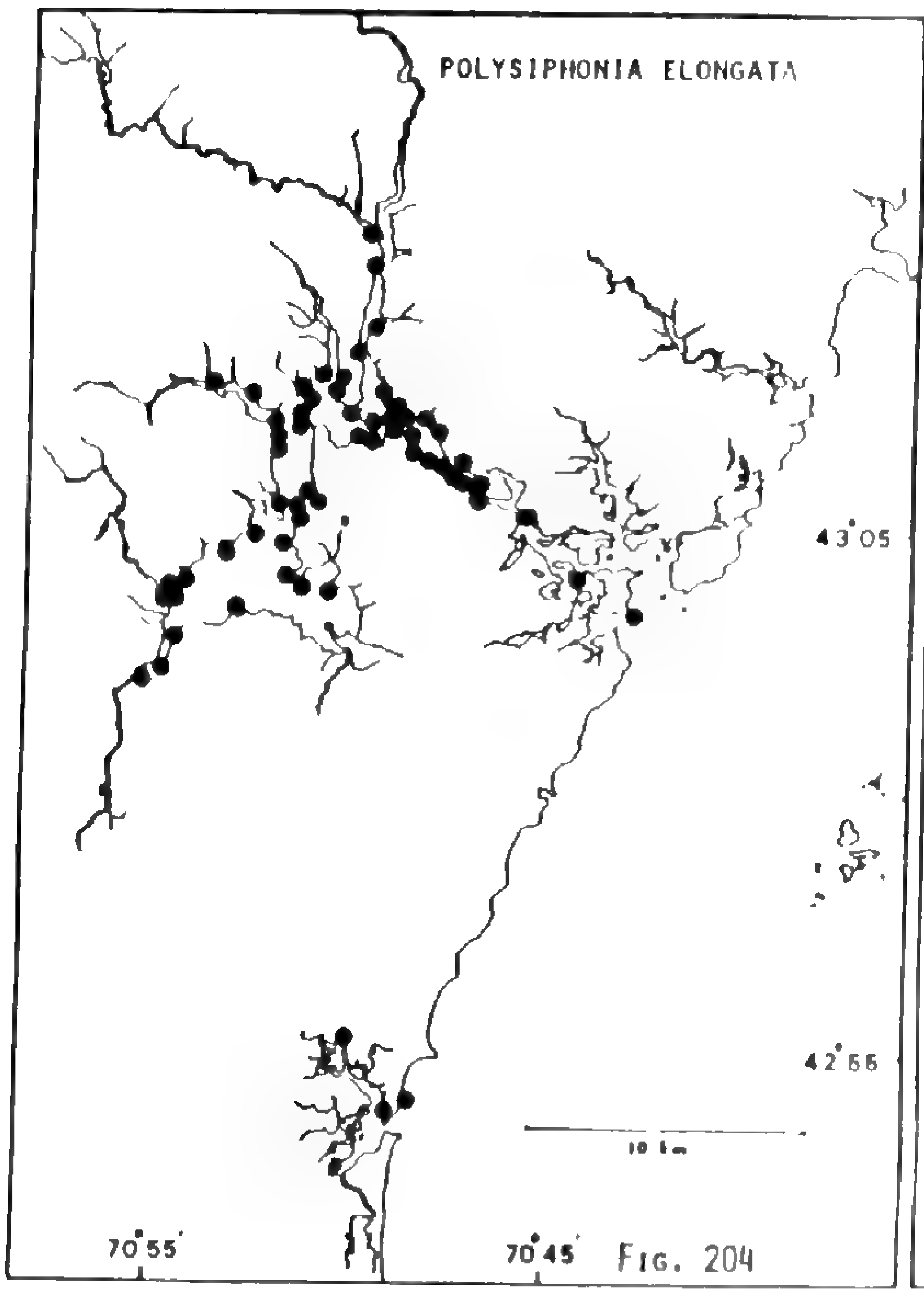

POLYSIPHONIA ELONGATA

FIG. 204

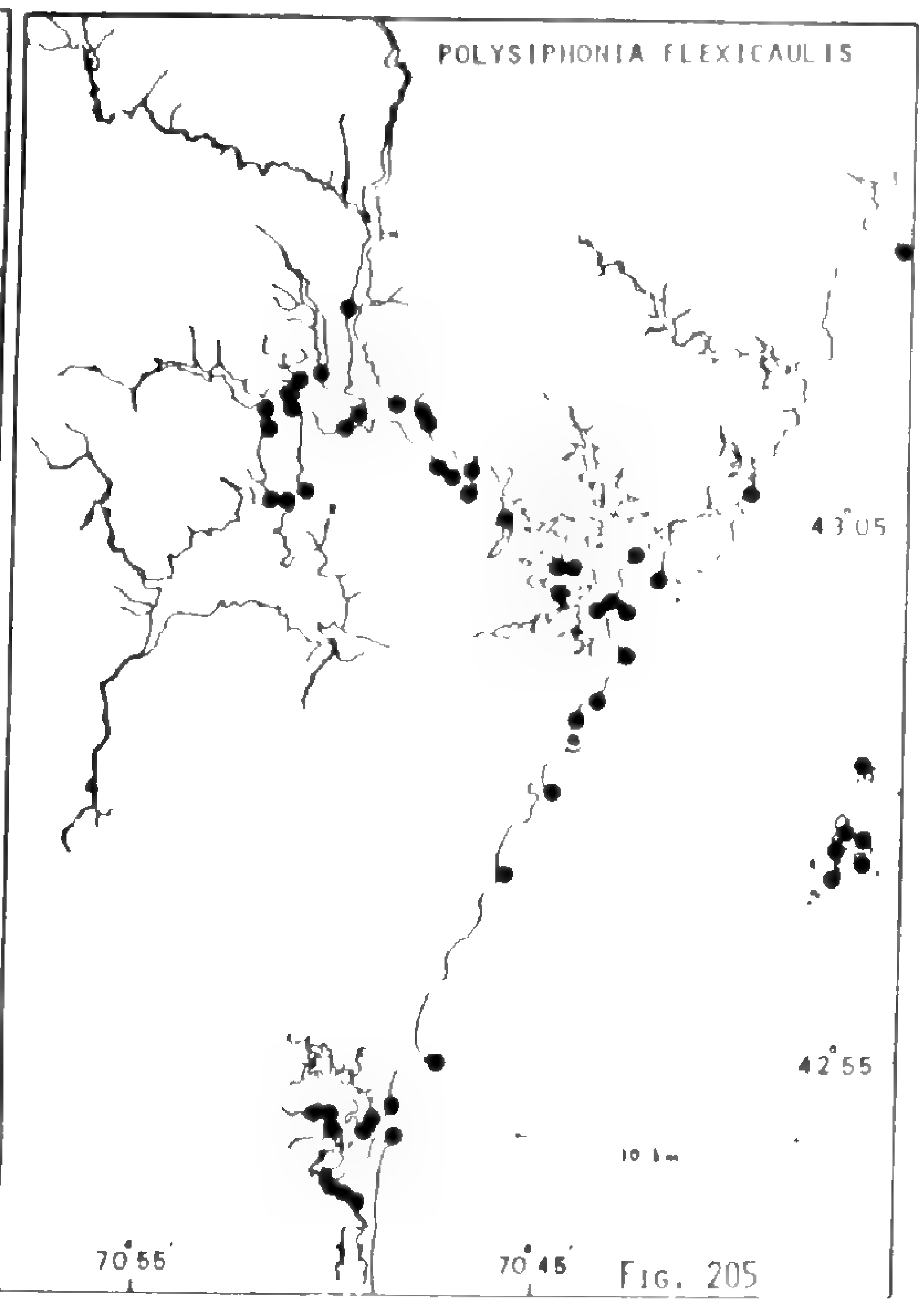

POLYSIPHONIA FLEXICAULIS

FIG. 205

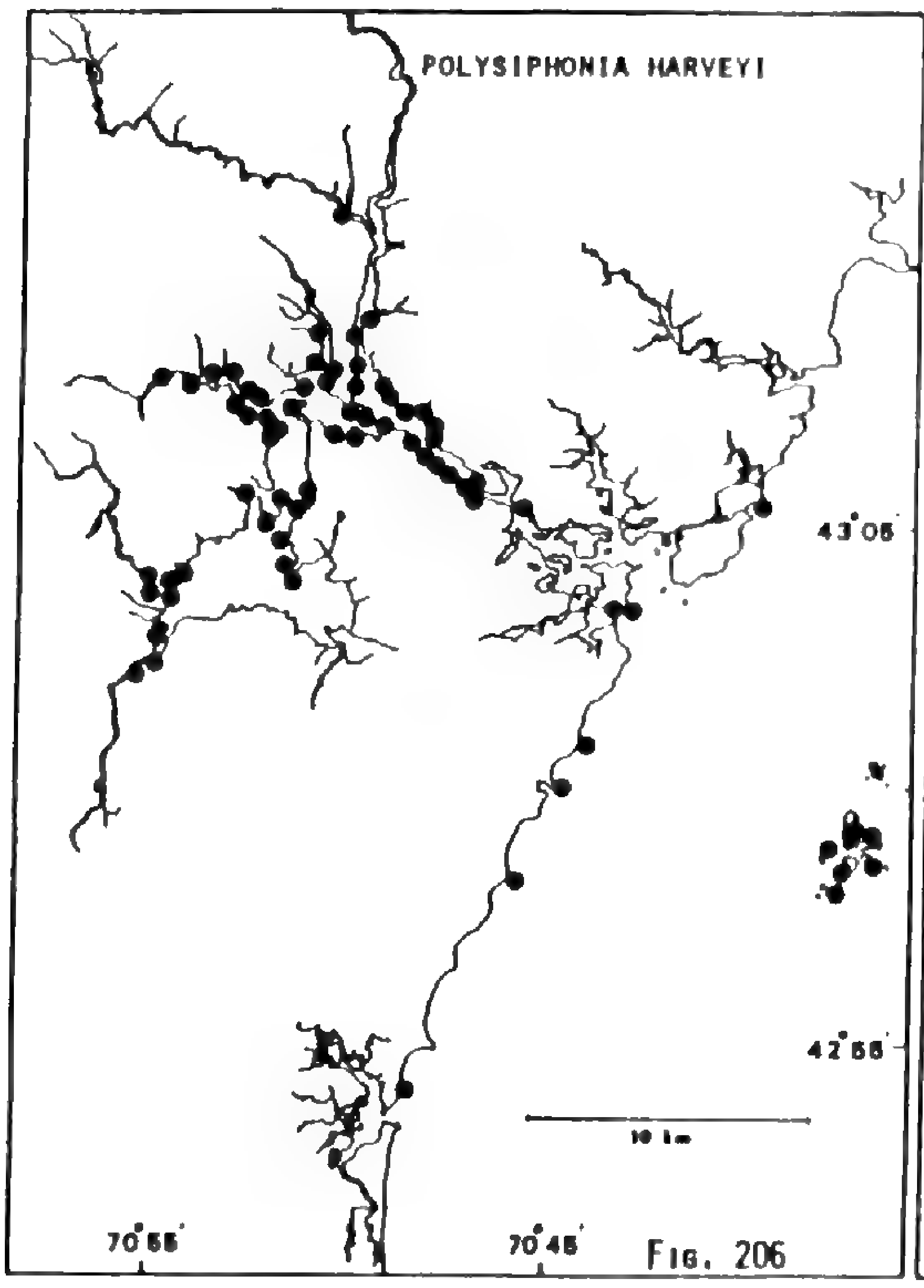

POLYSIPHONIA HARVEYI

FIG. 206

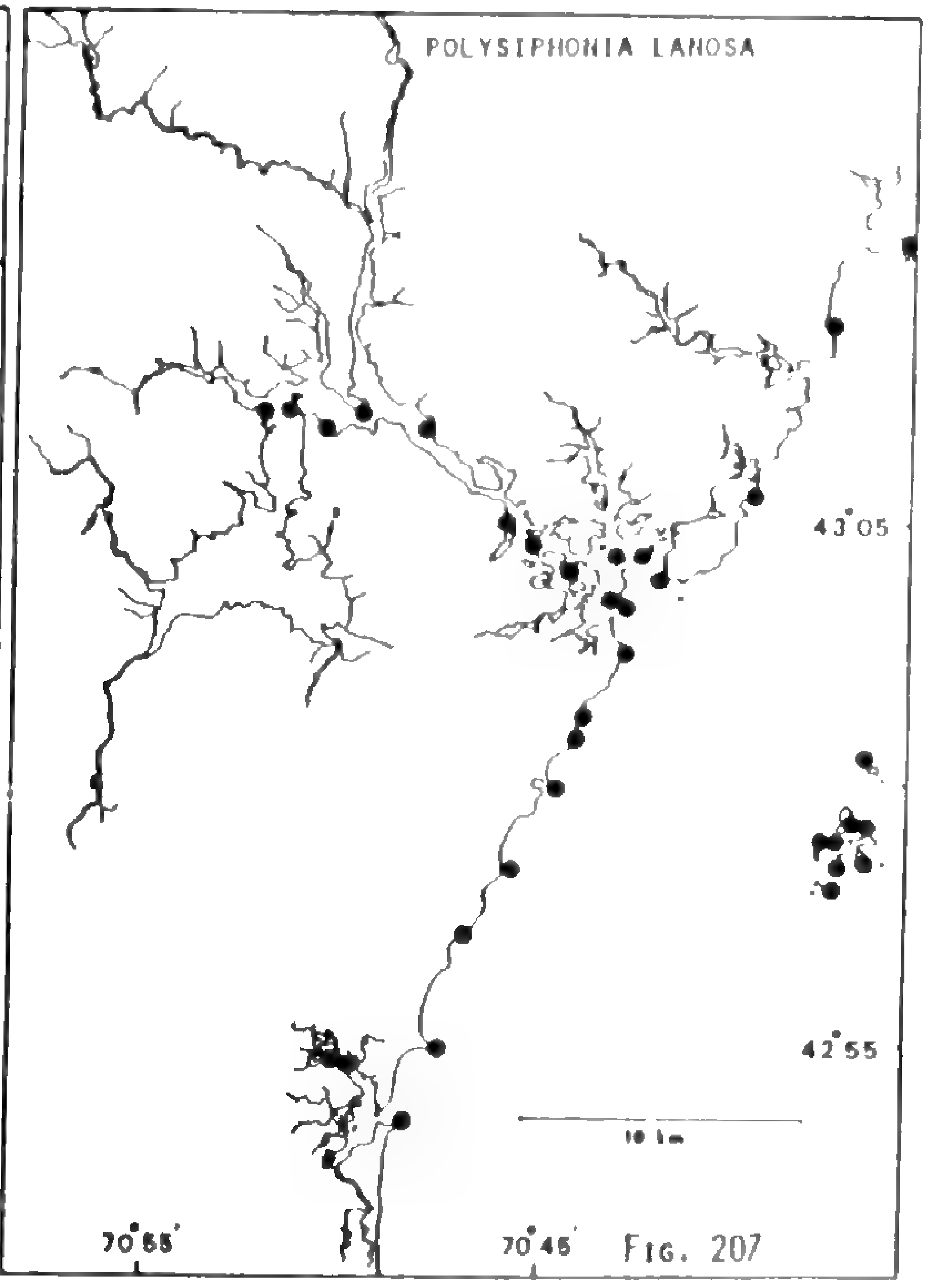

POLYSIPHONIA LANOSA

FIG. 207

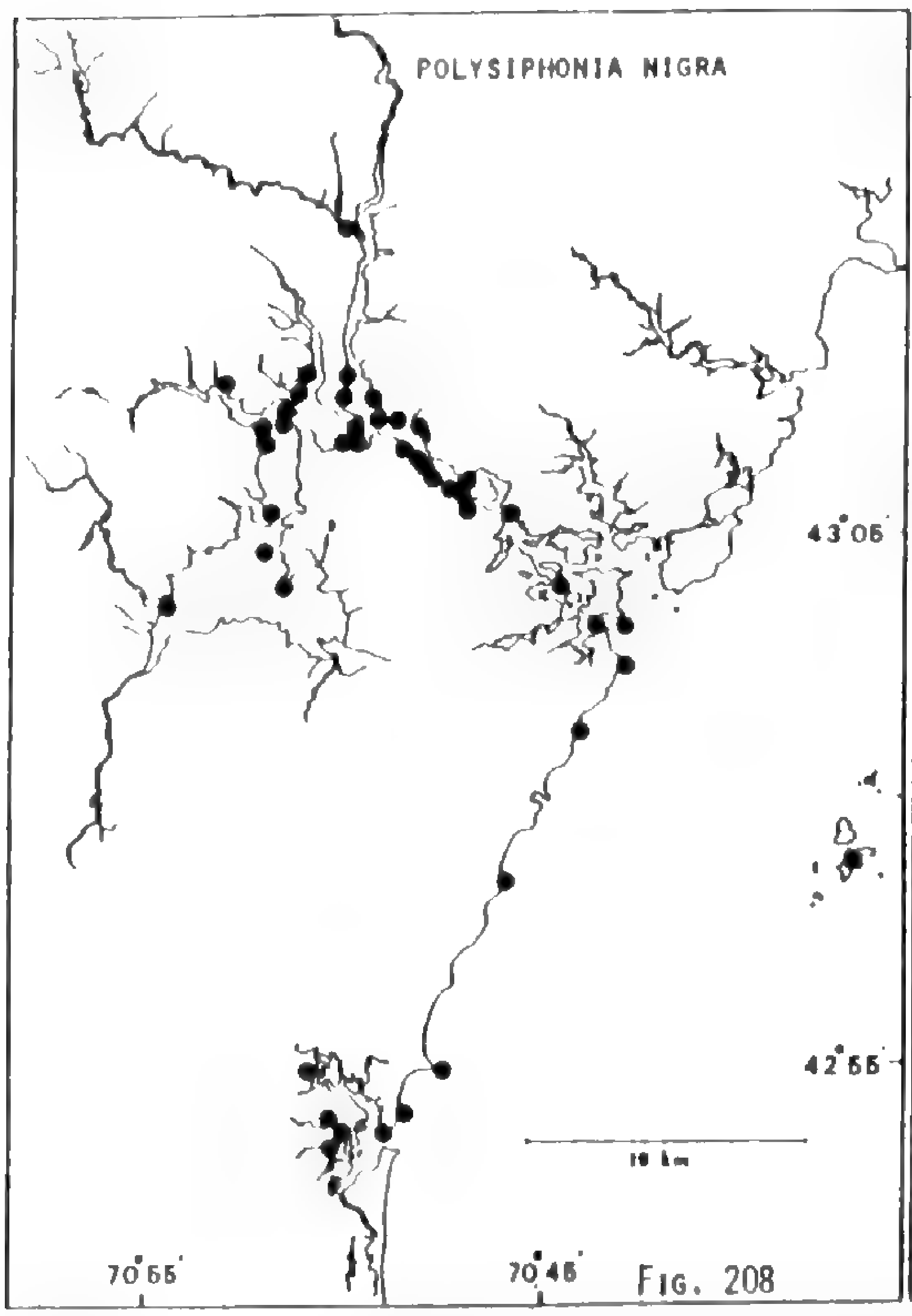


Fig. 208

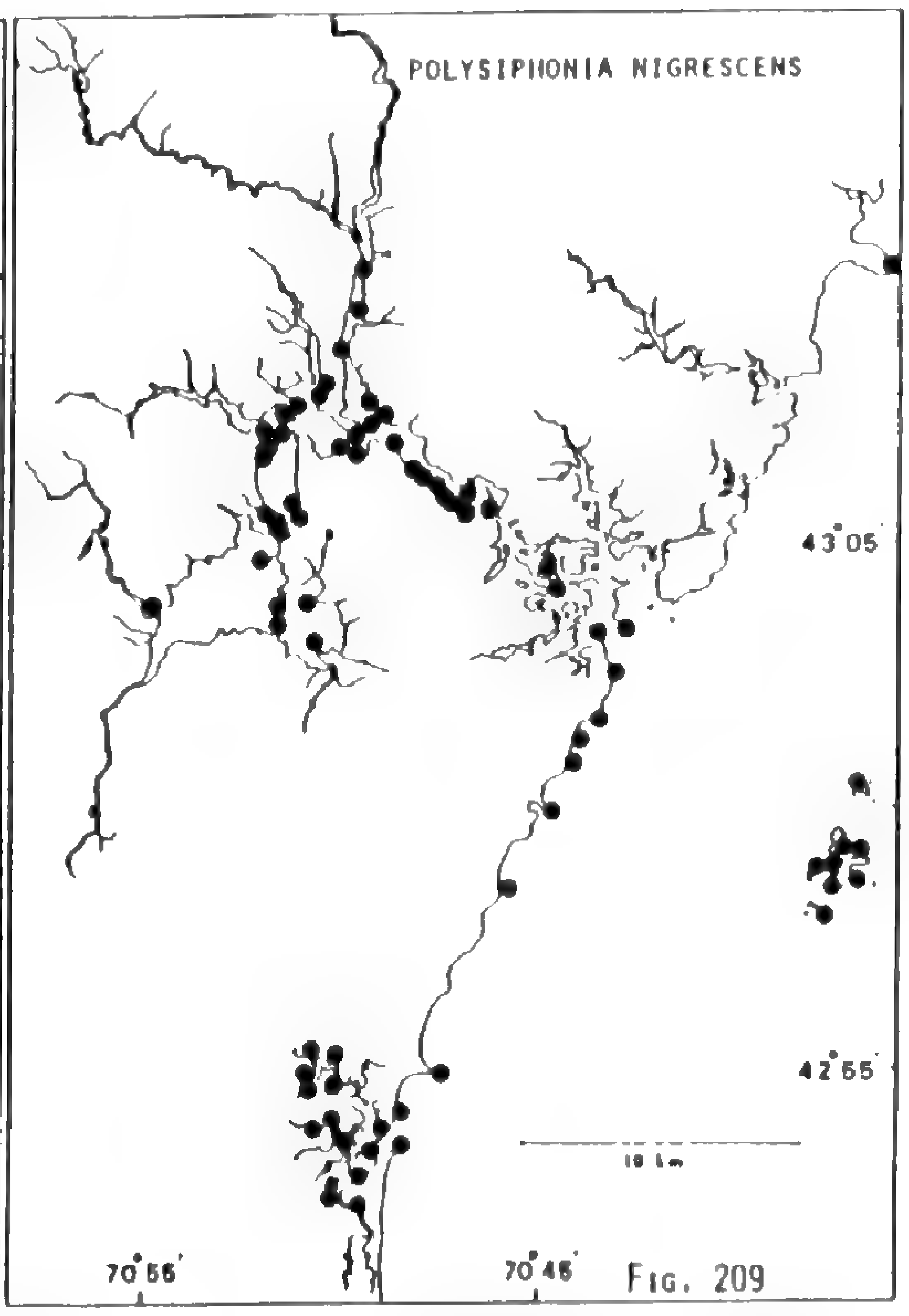
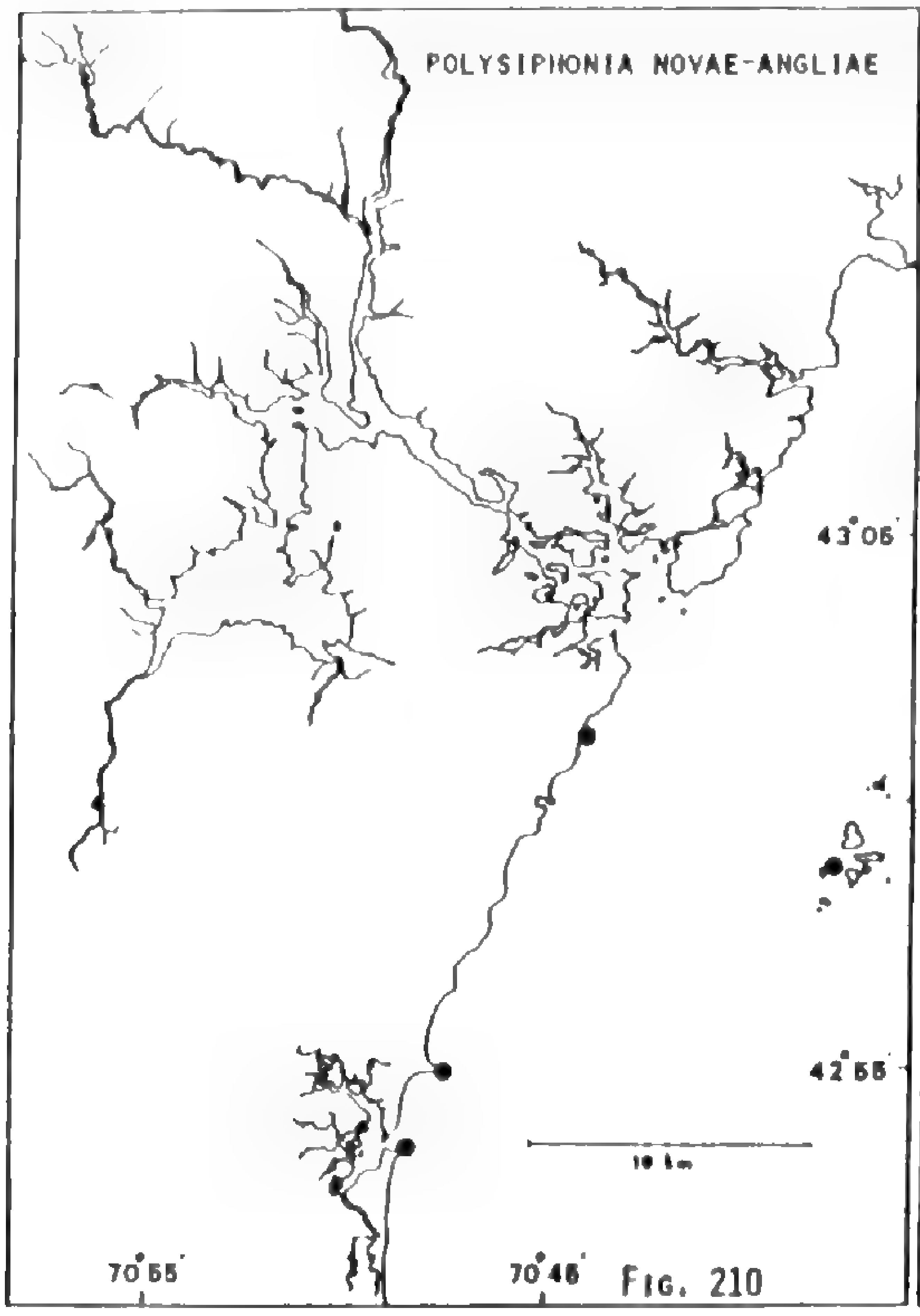


Fig. 209



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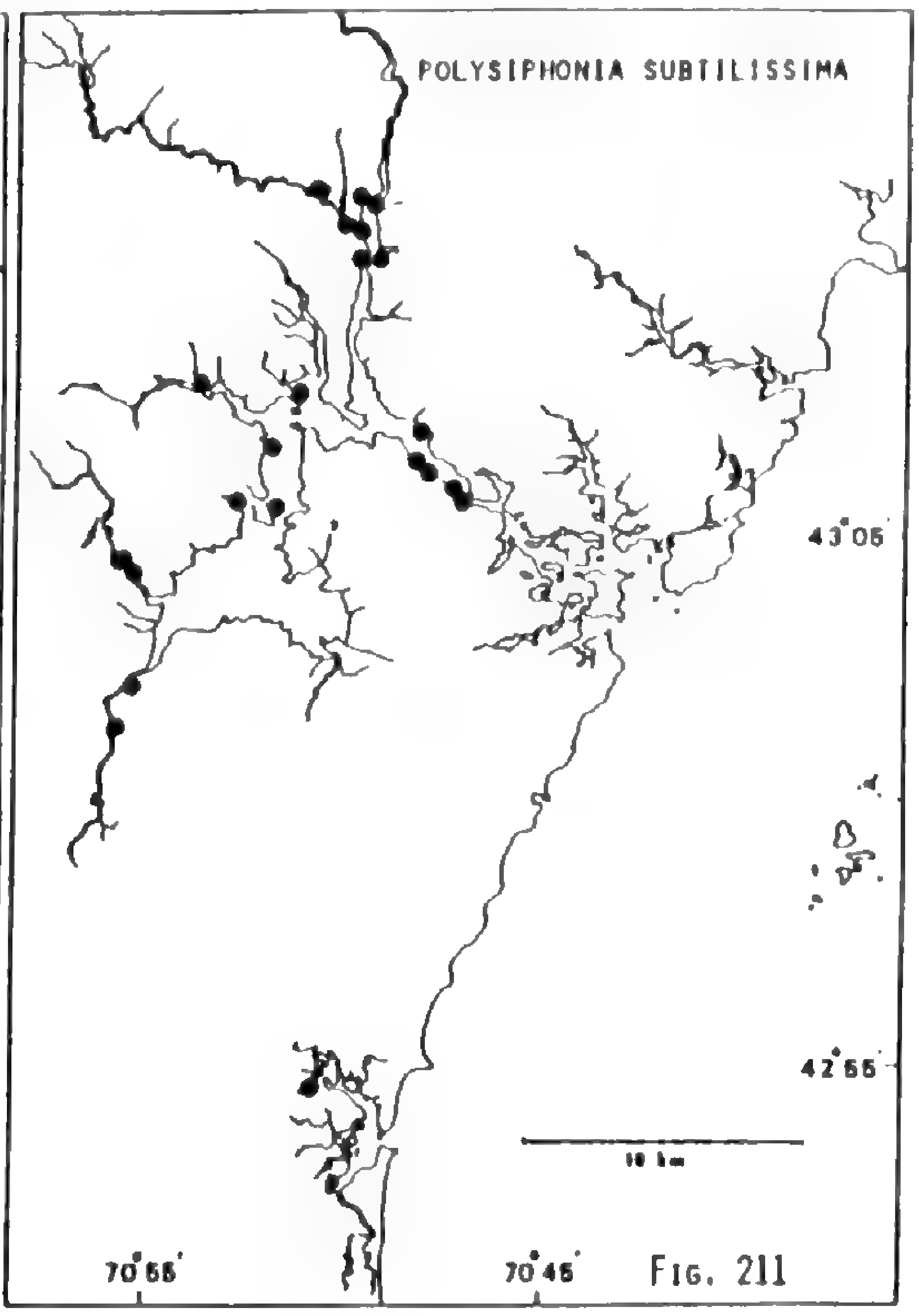

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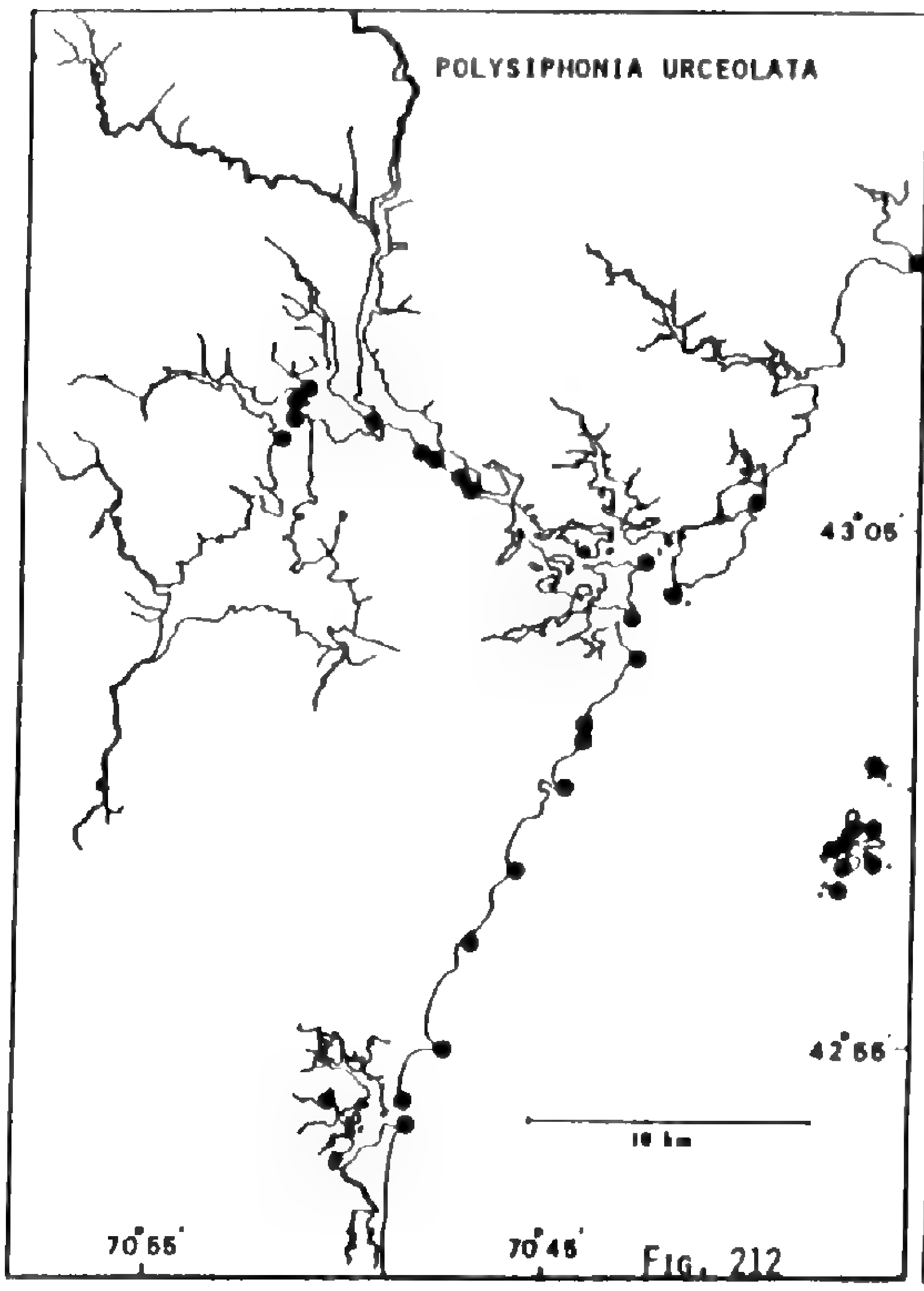


Fig. 212

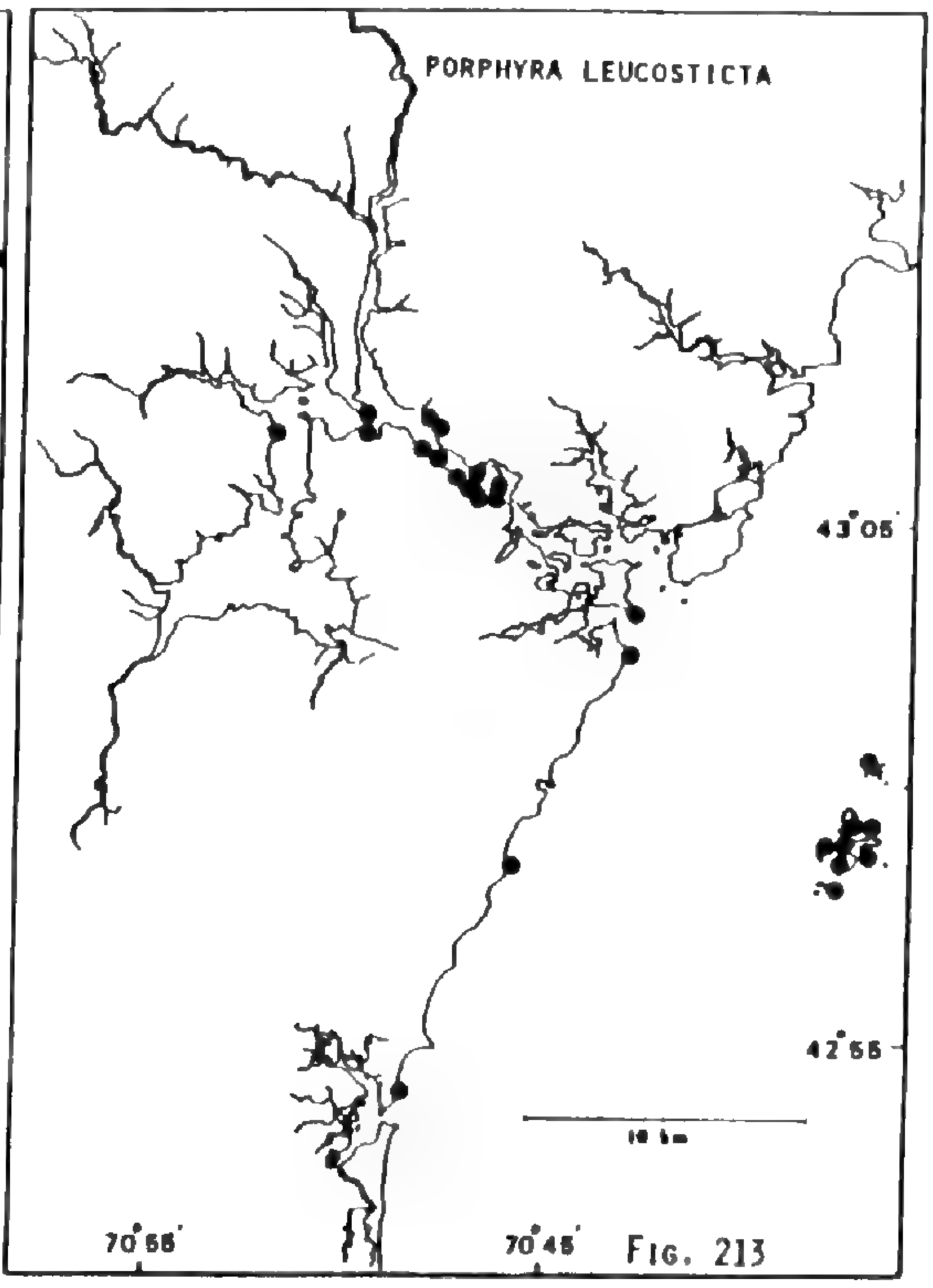
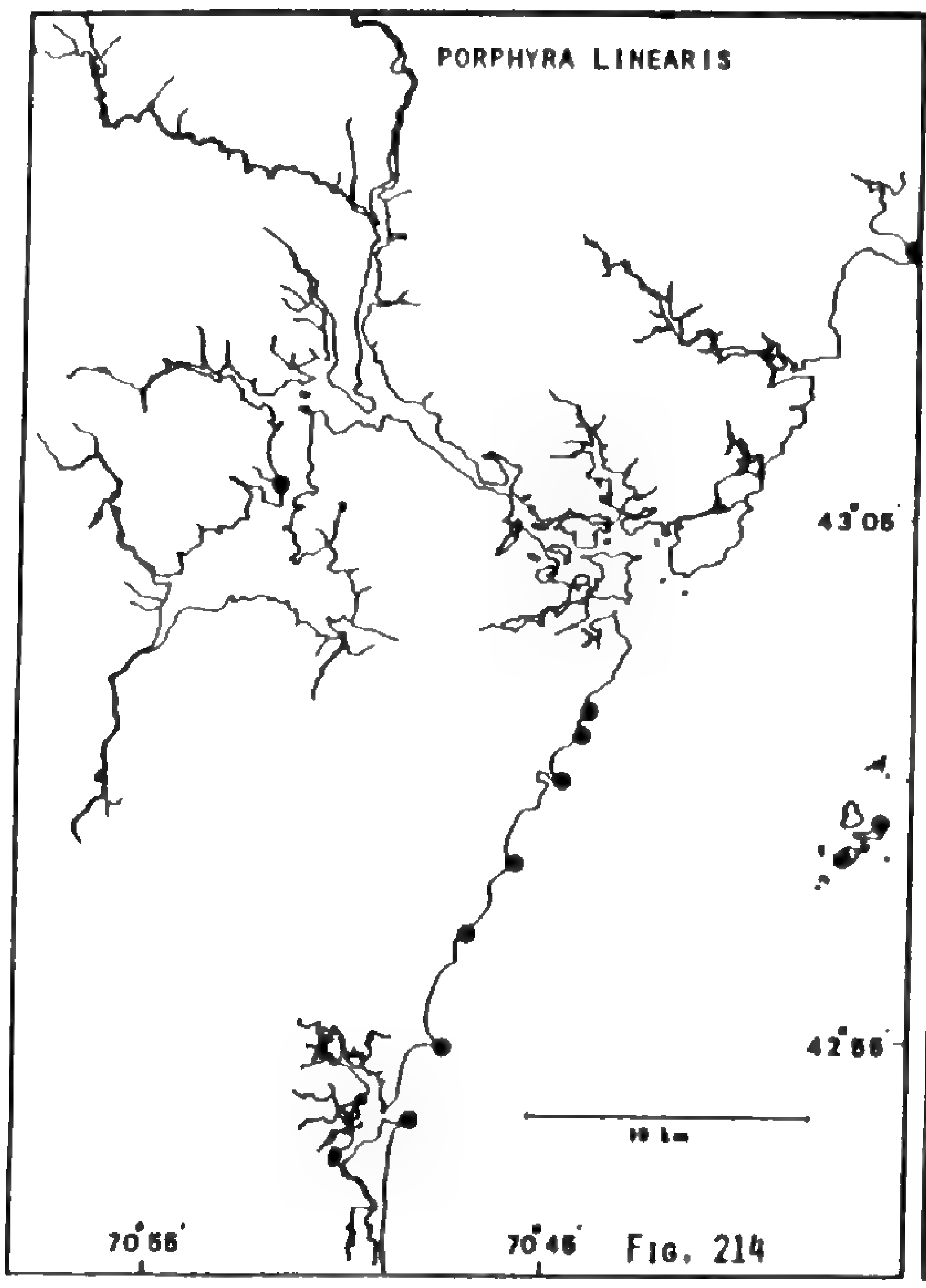


Fig. 213



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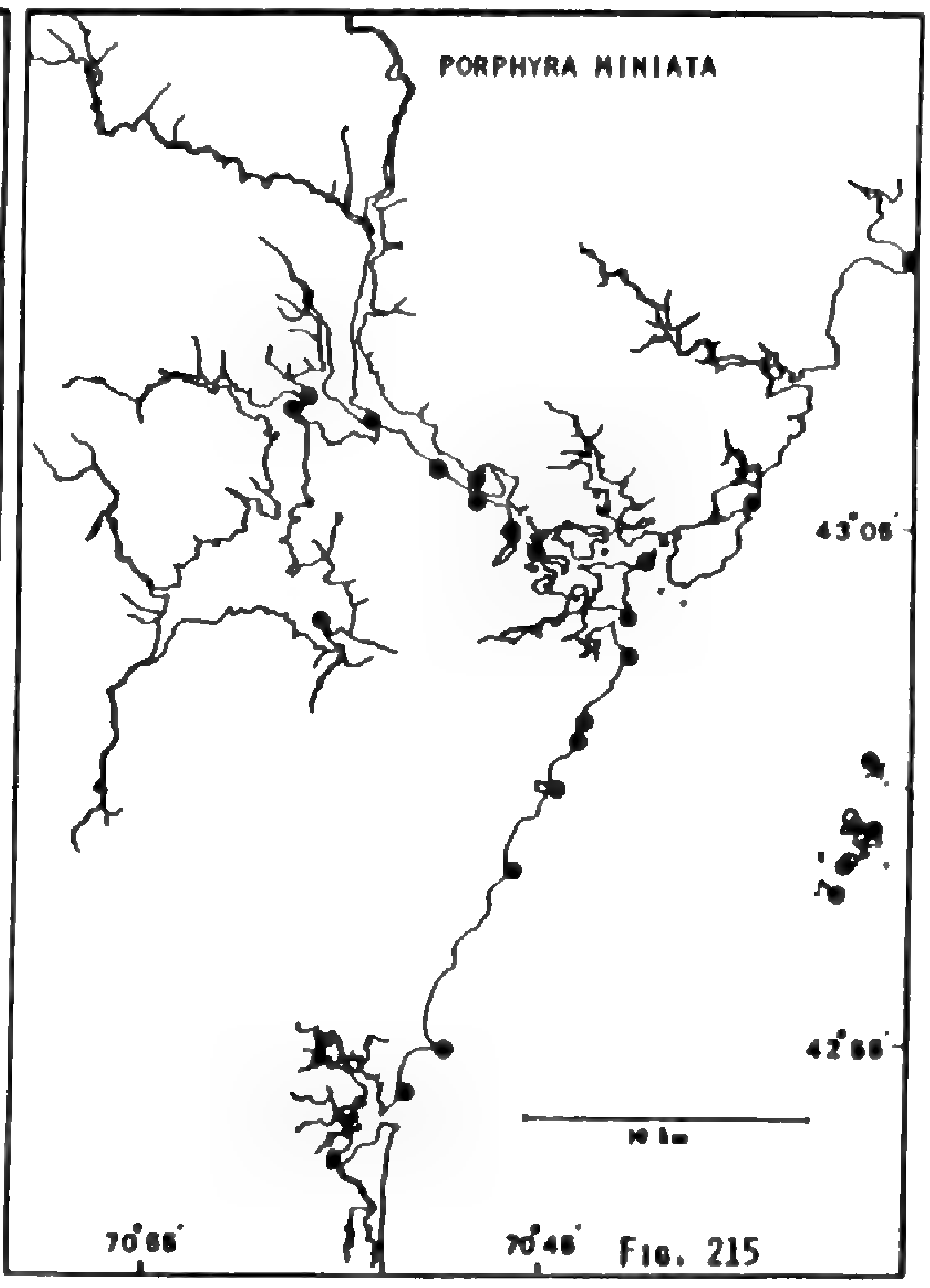

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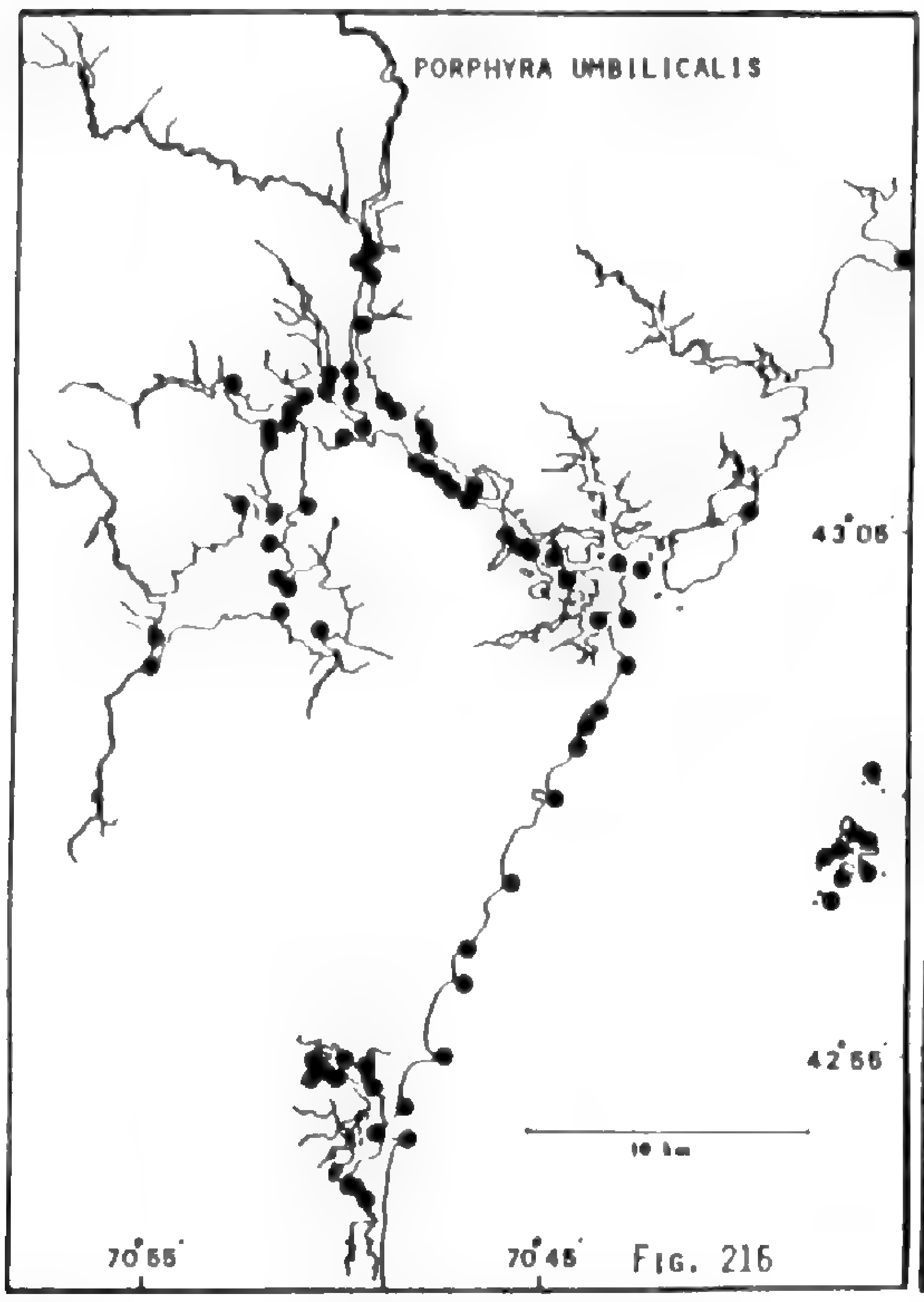
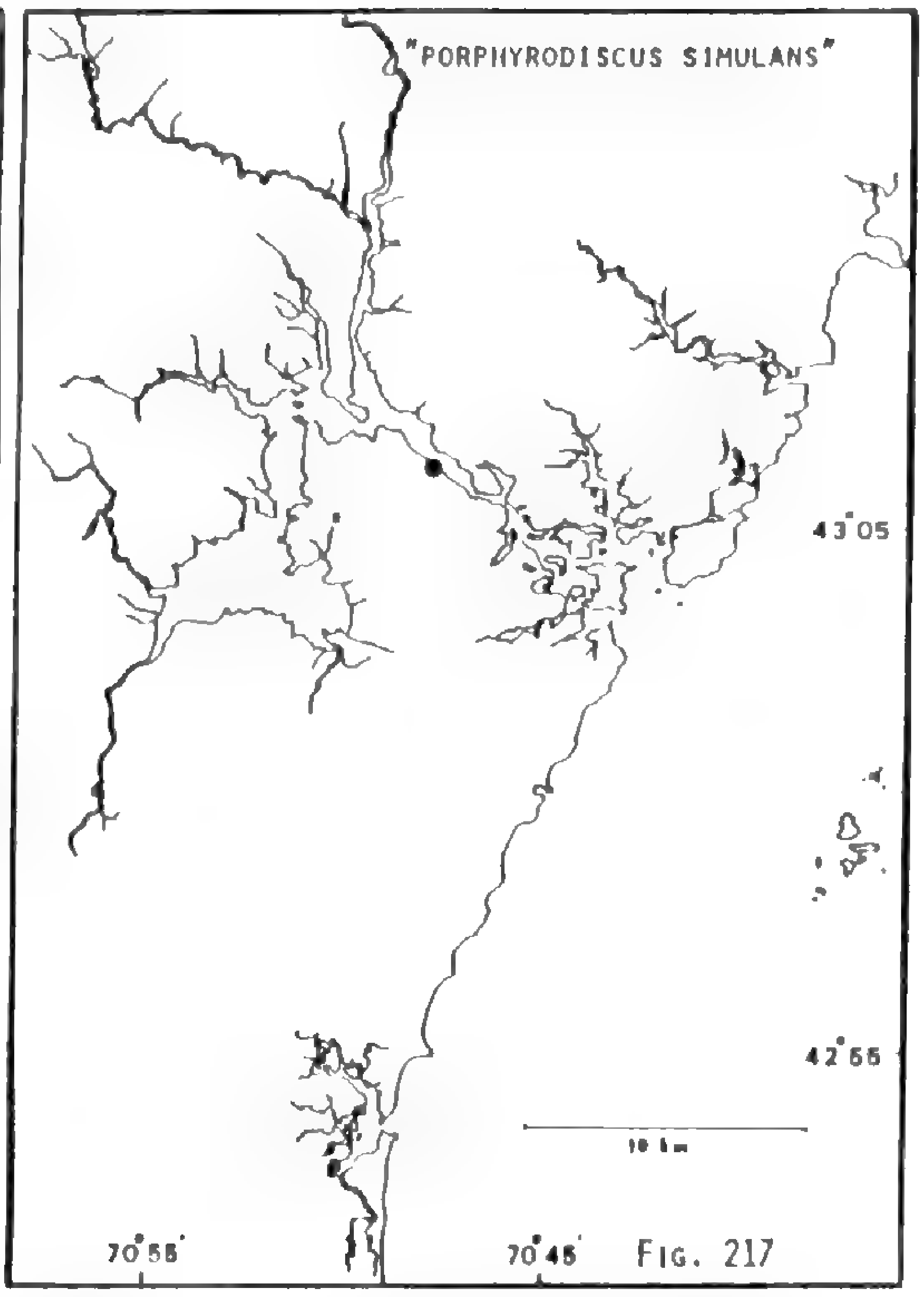


FIG. 216



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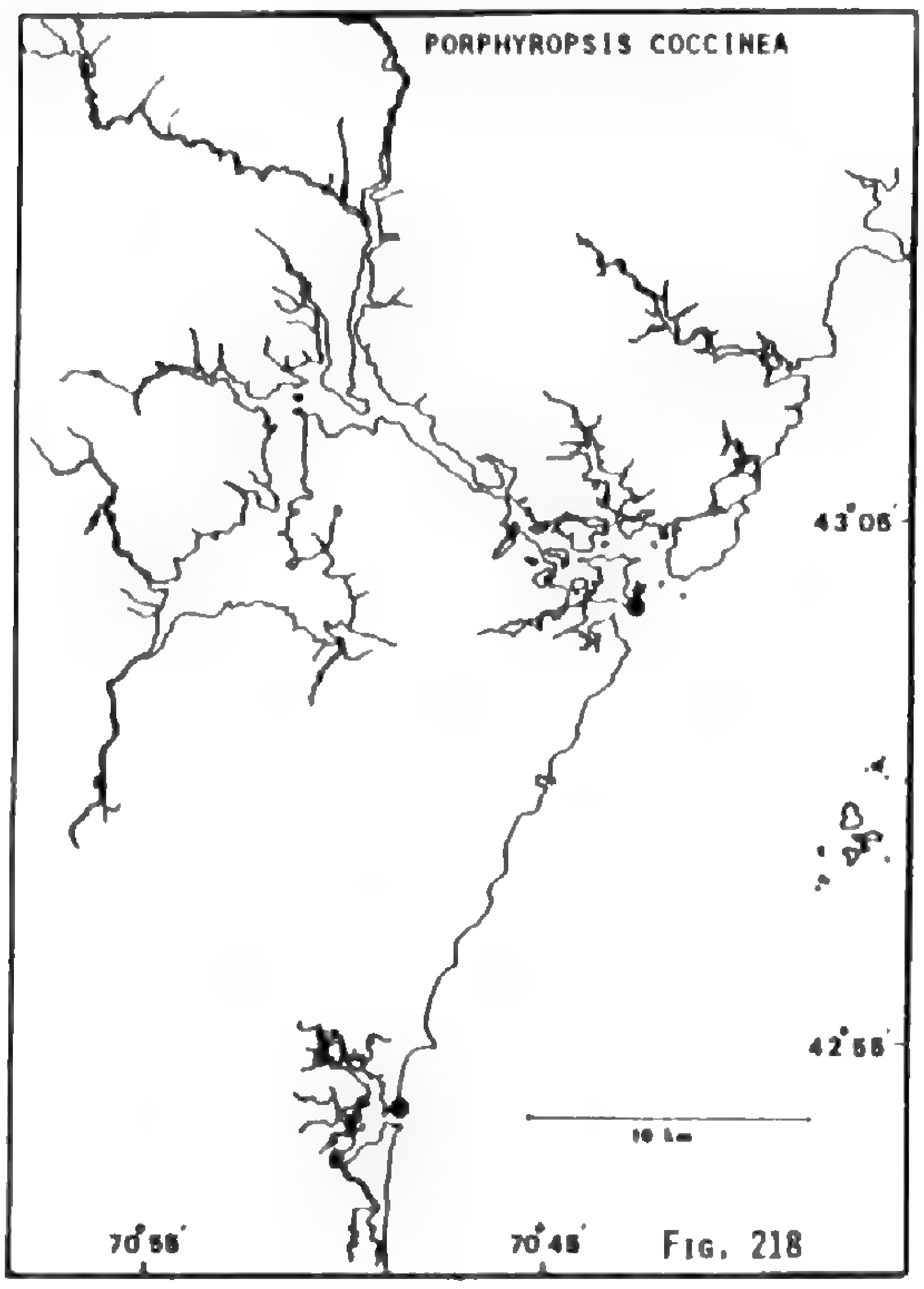

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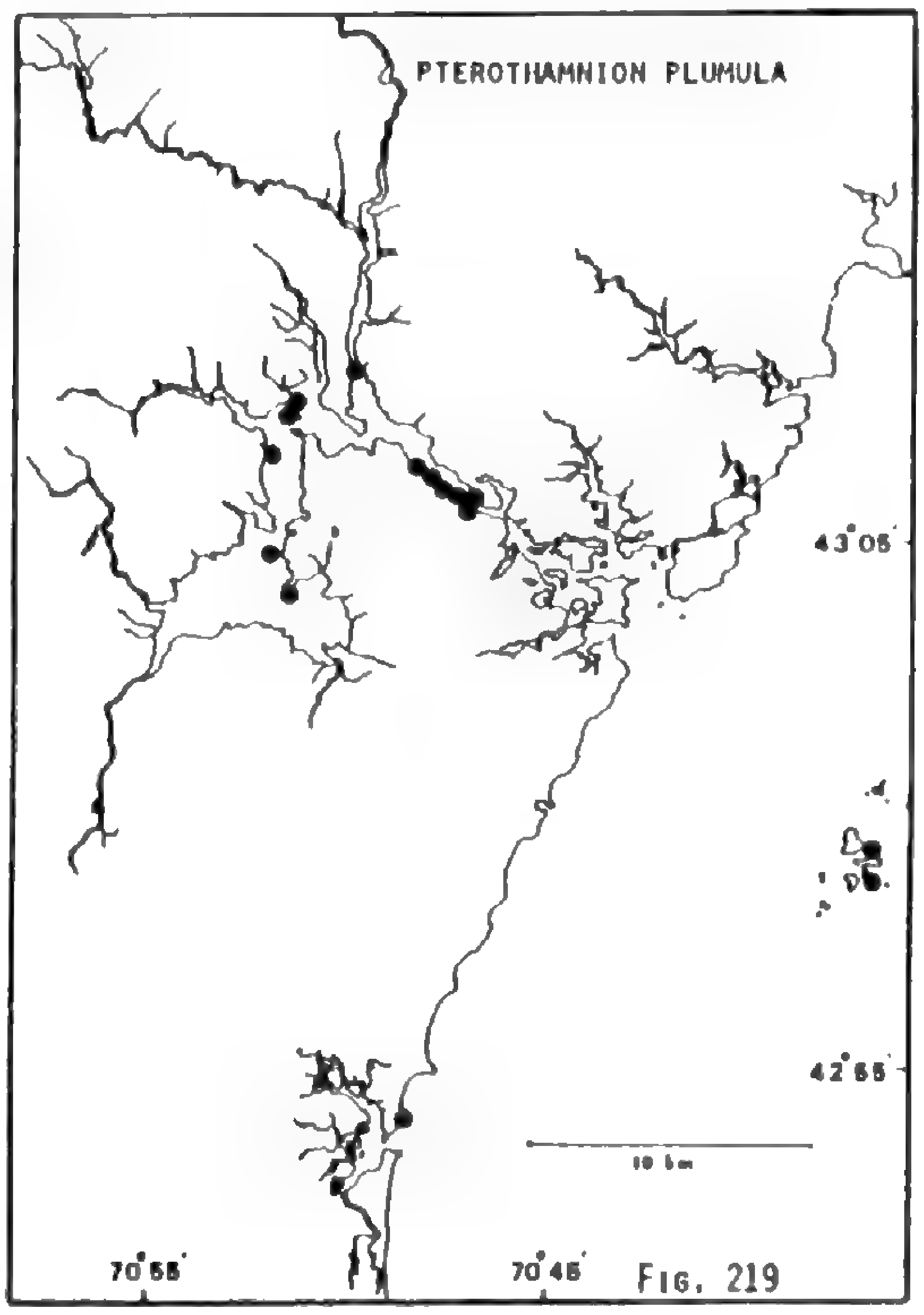

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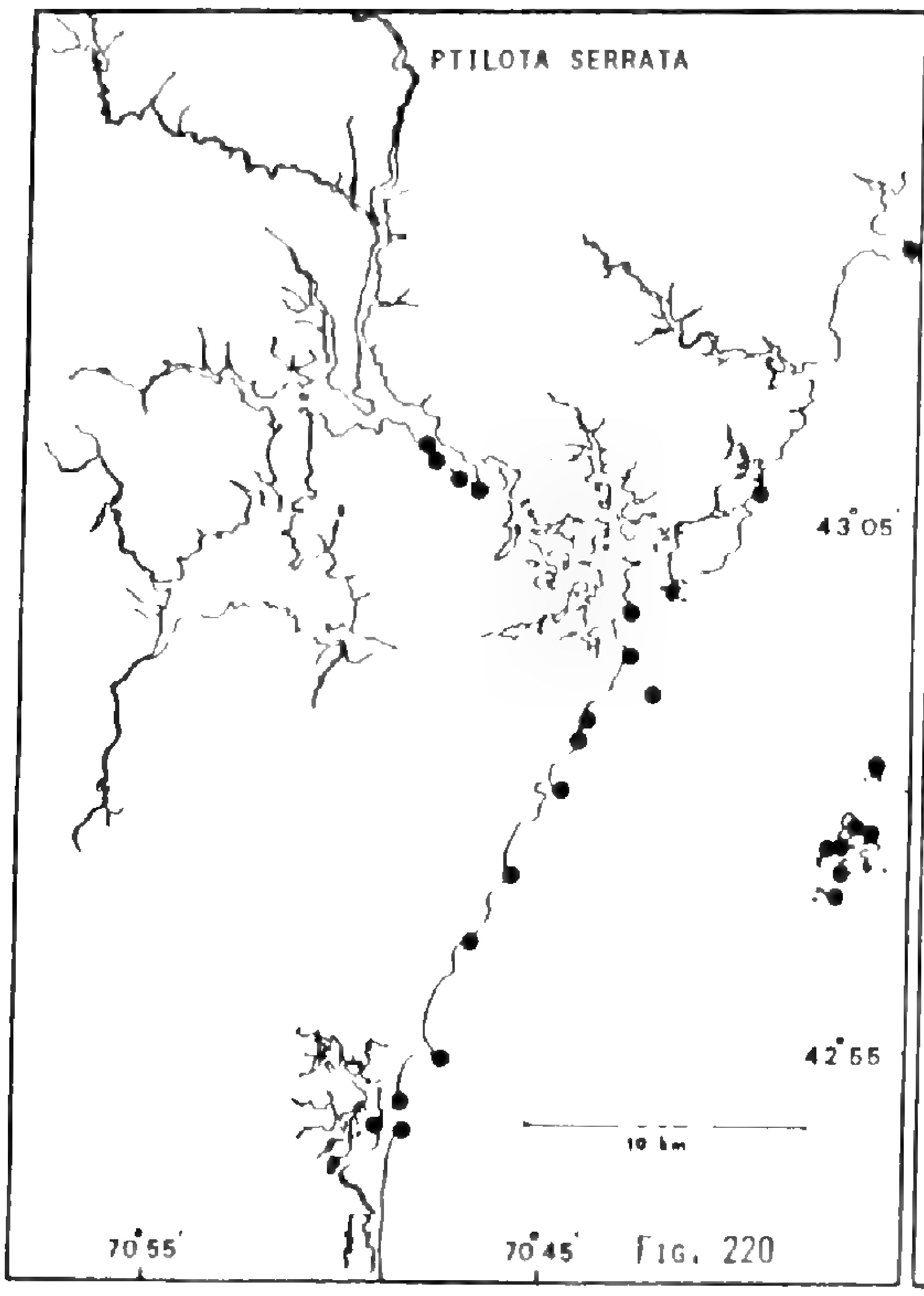

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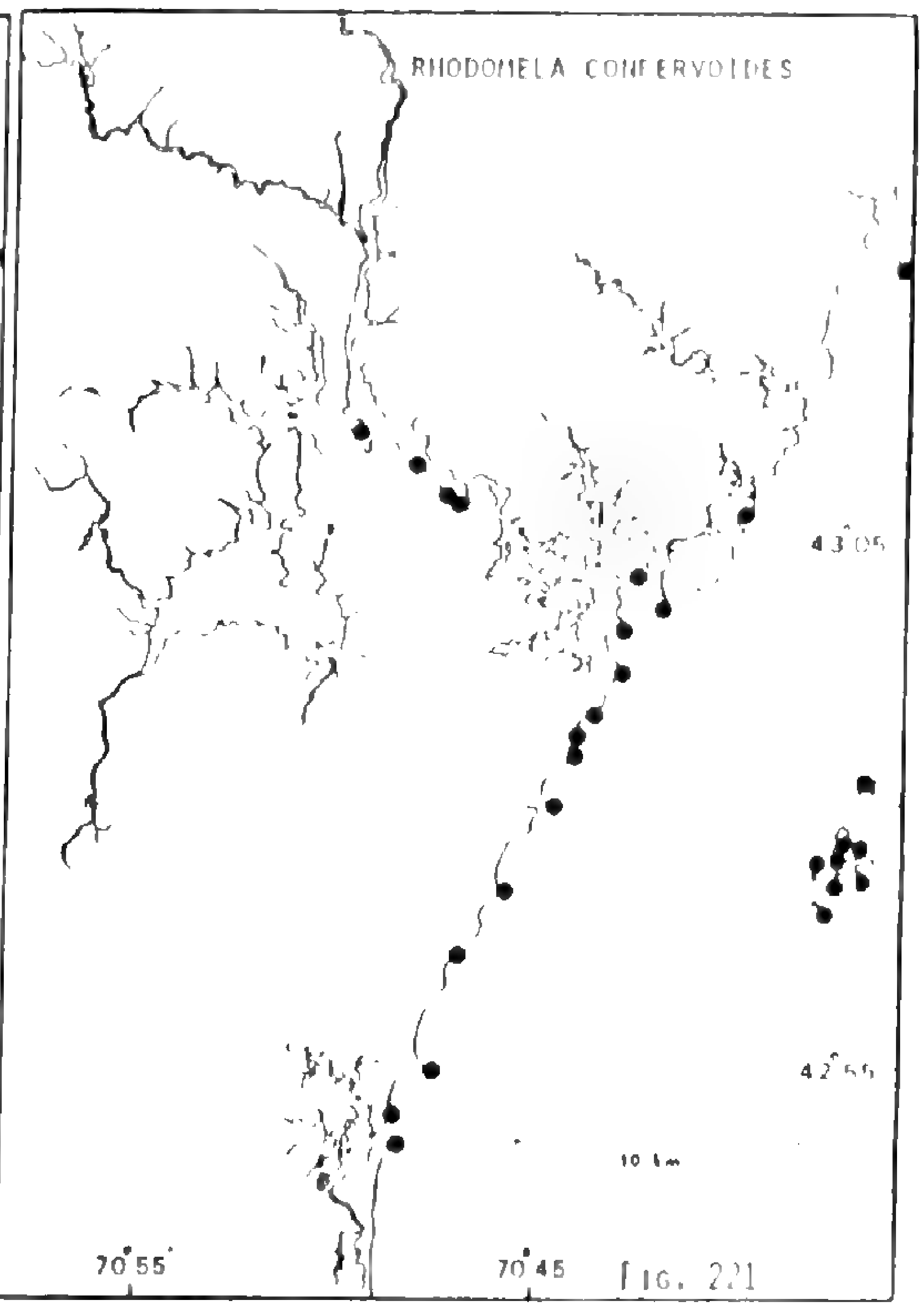


FIG. 221

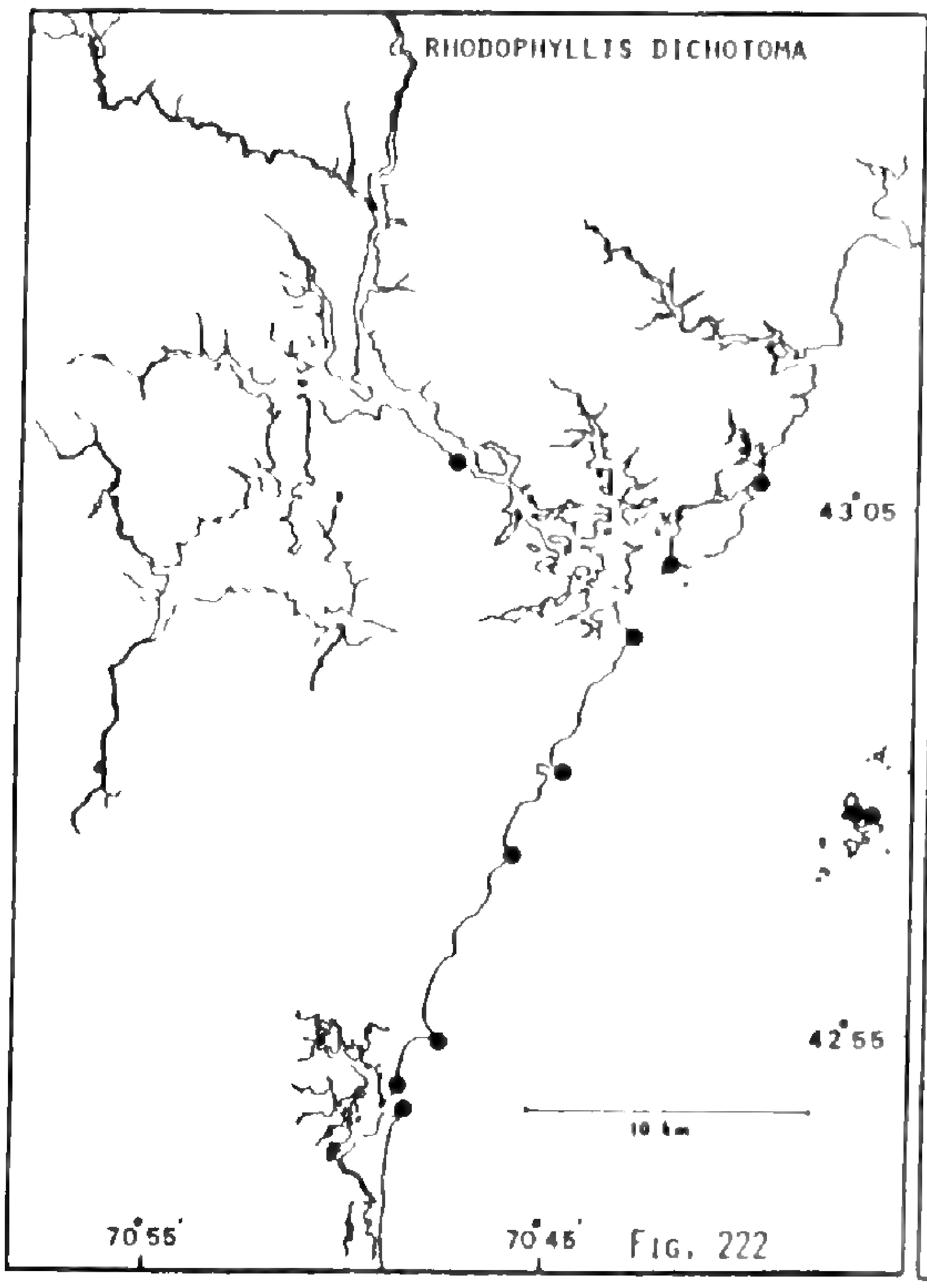
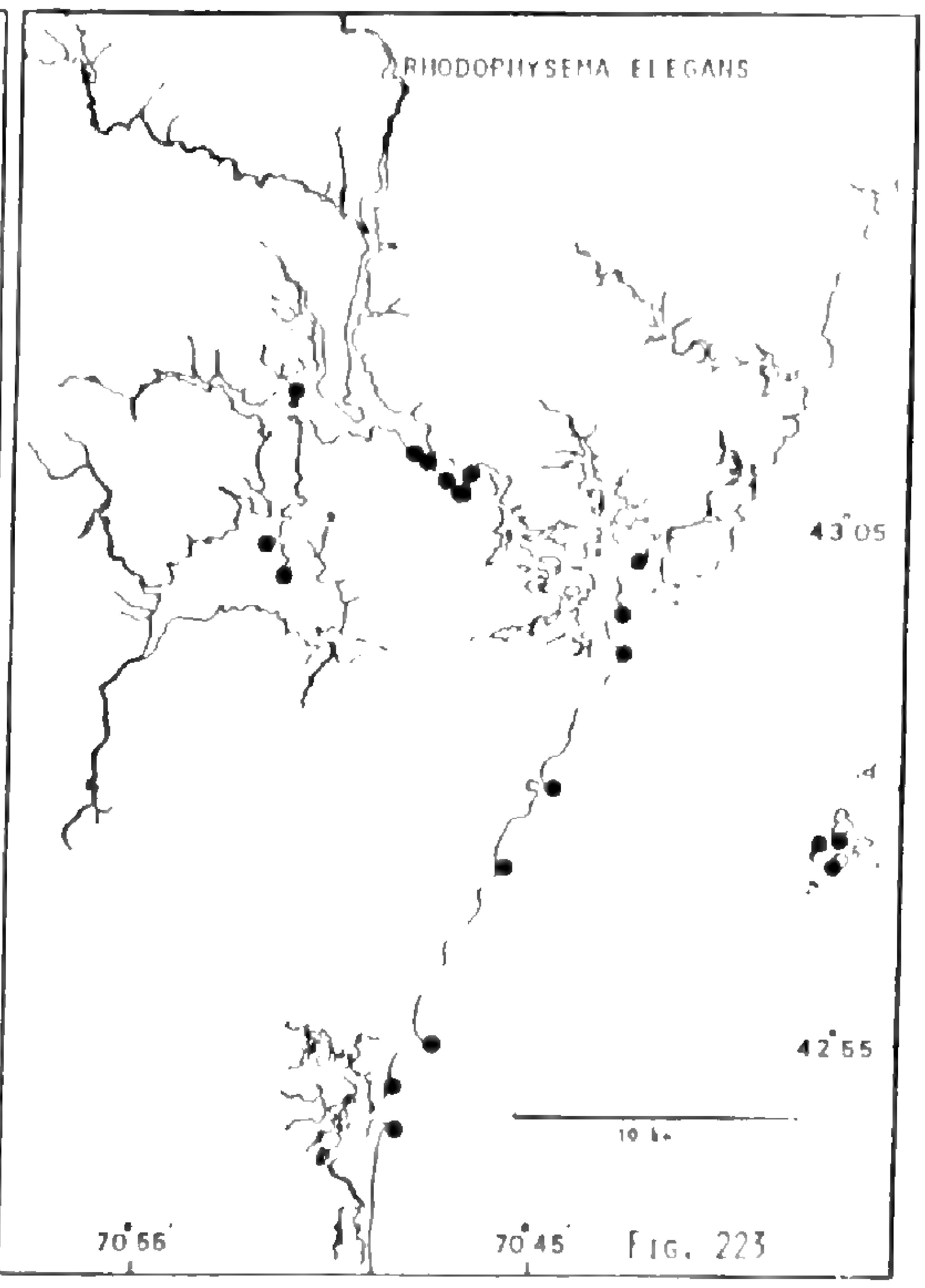


FIG. 222



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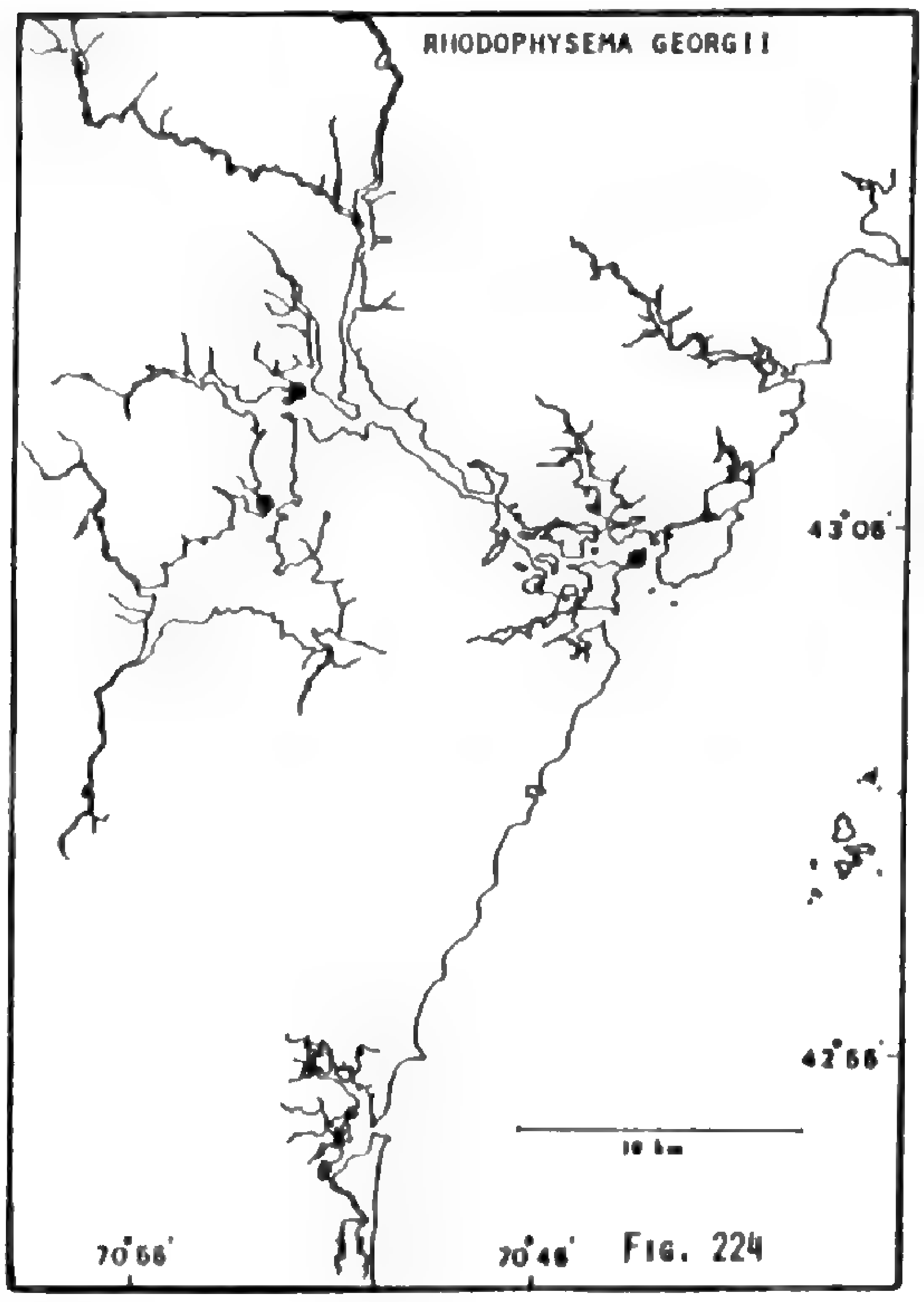


FIG. 224

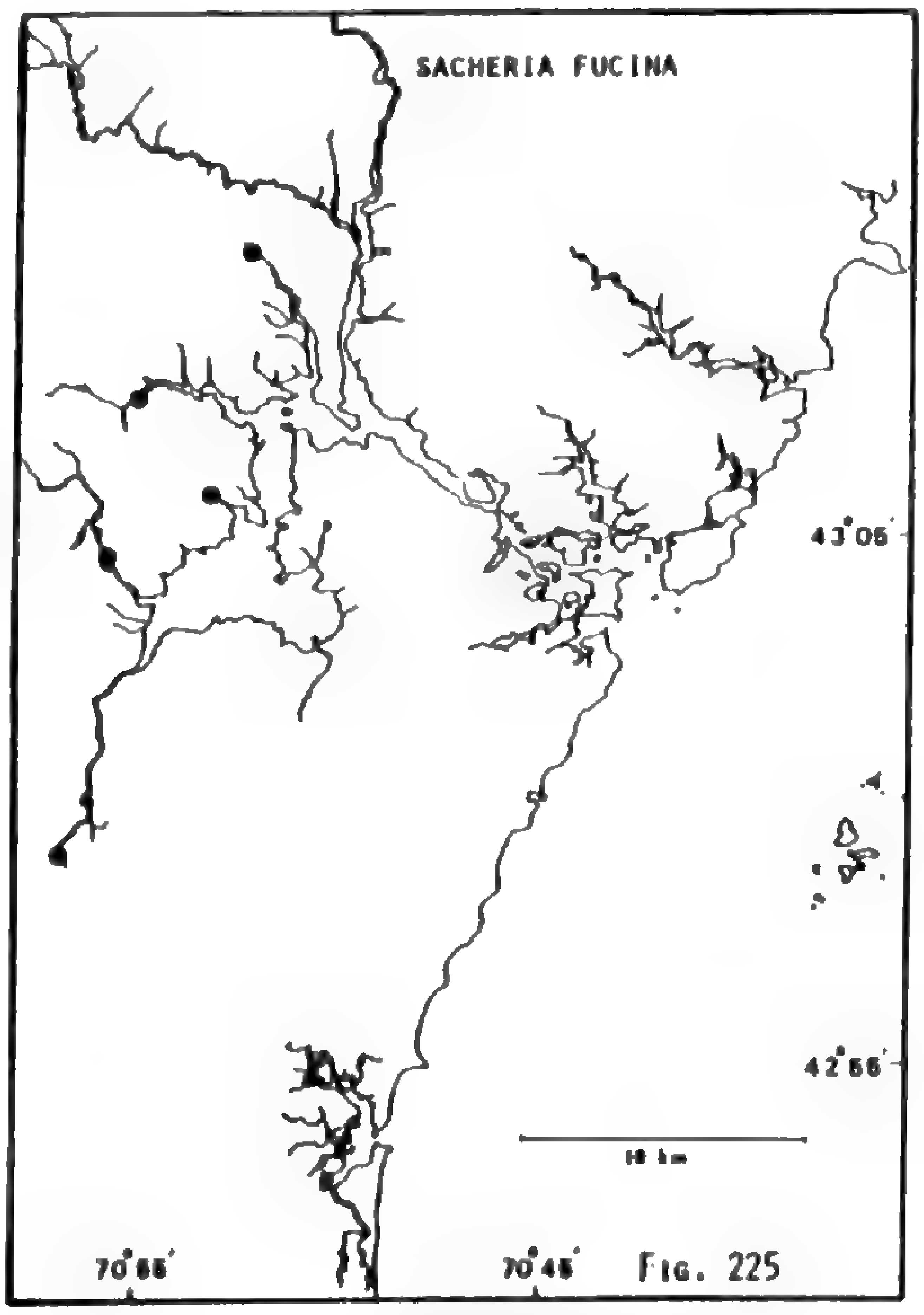


FIG. 225

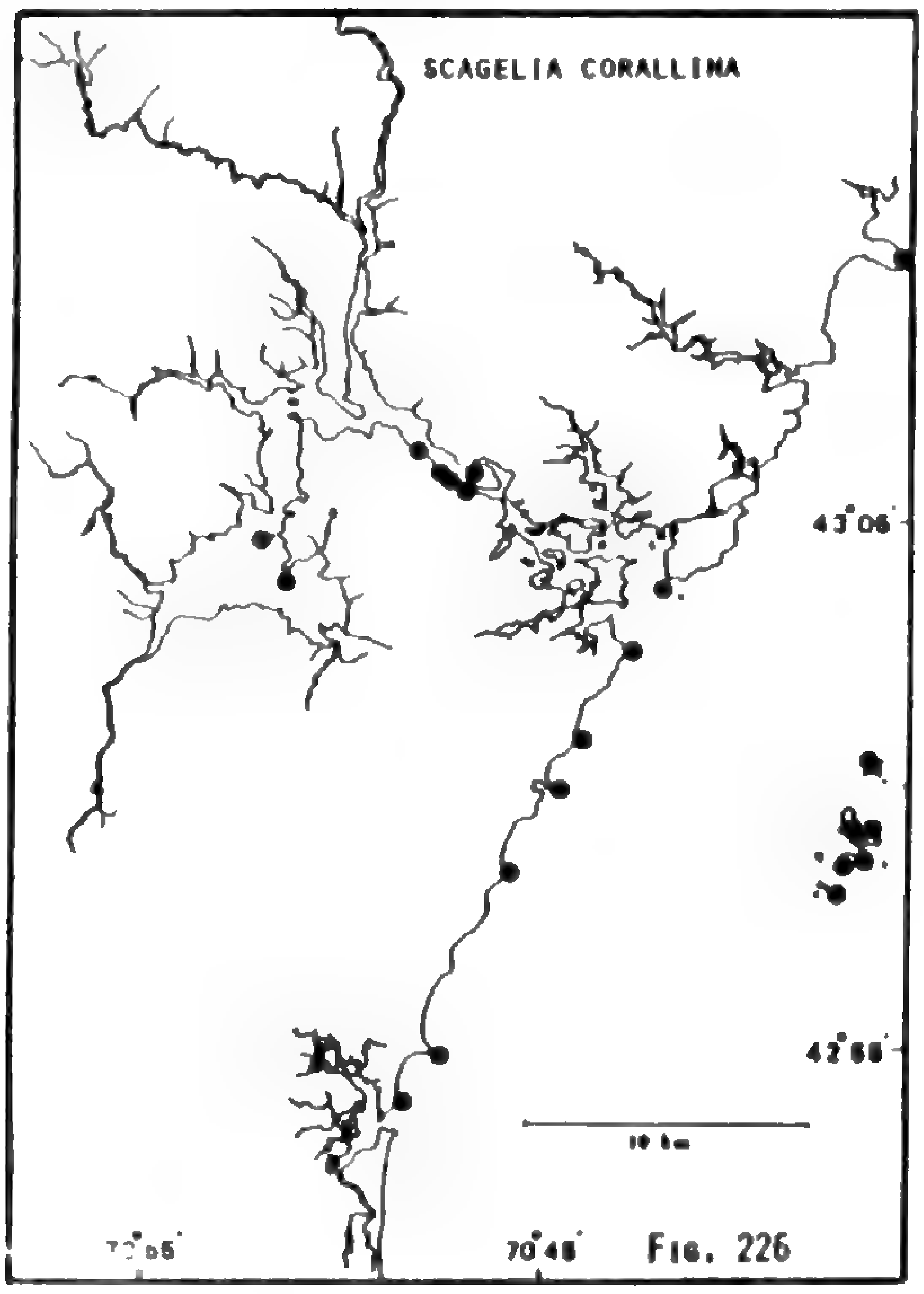


FIG. 226

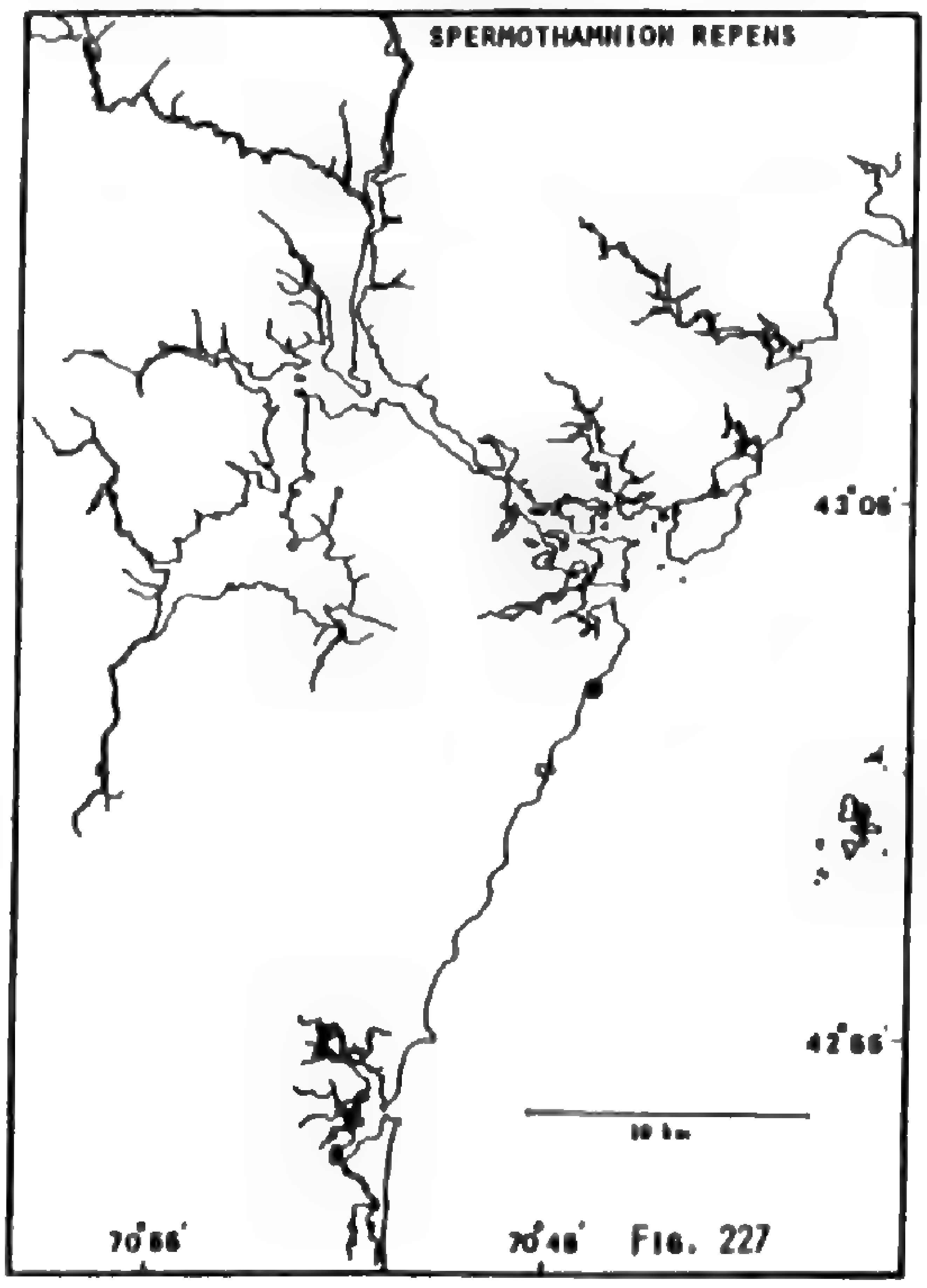


FIG. 227

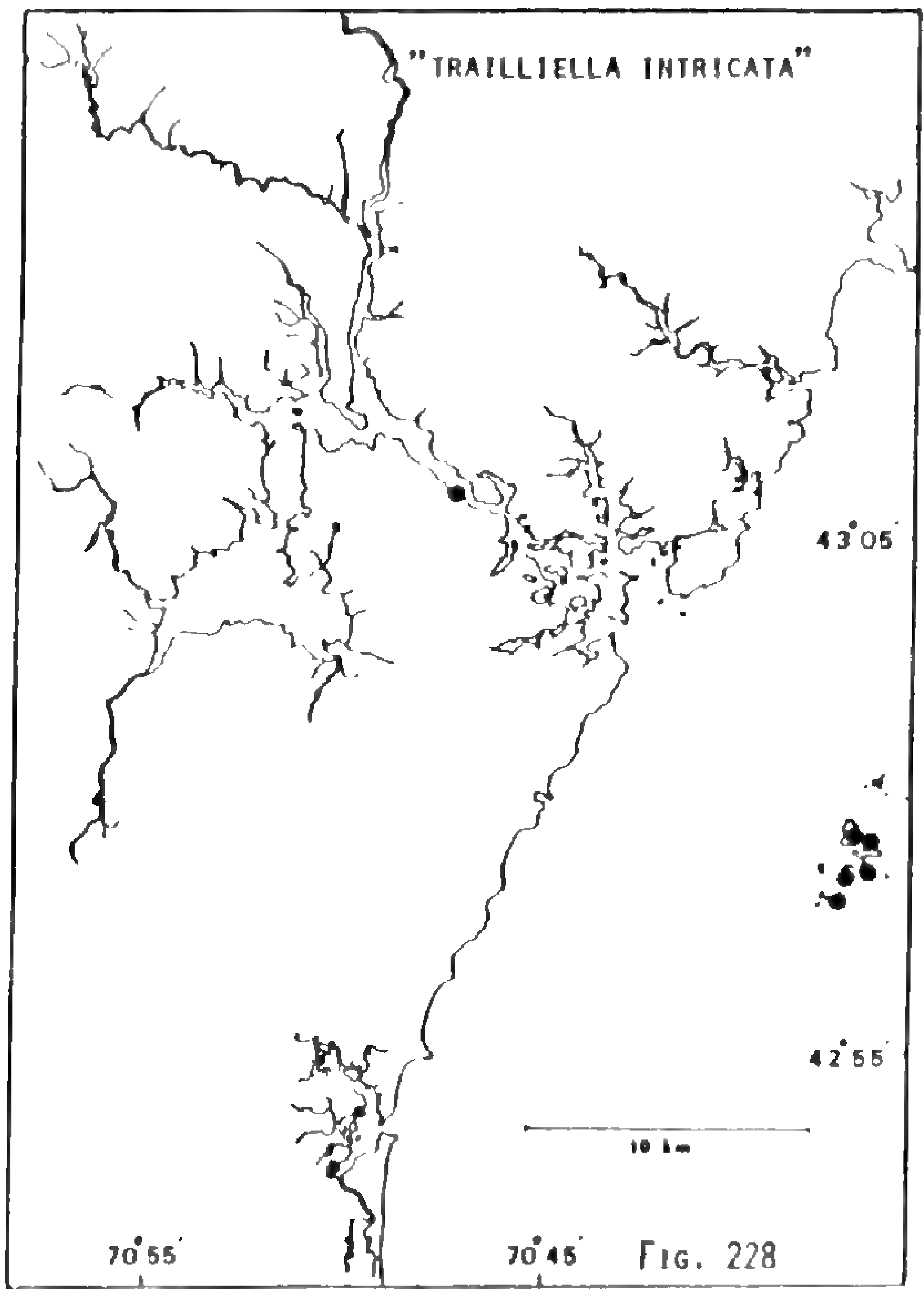


FIG. 228

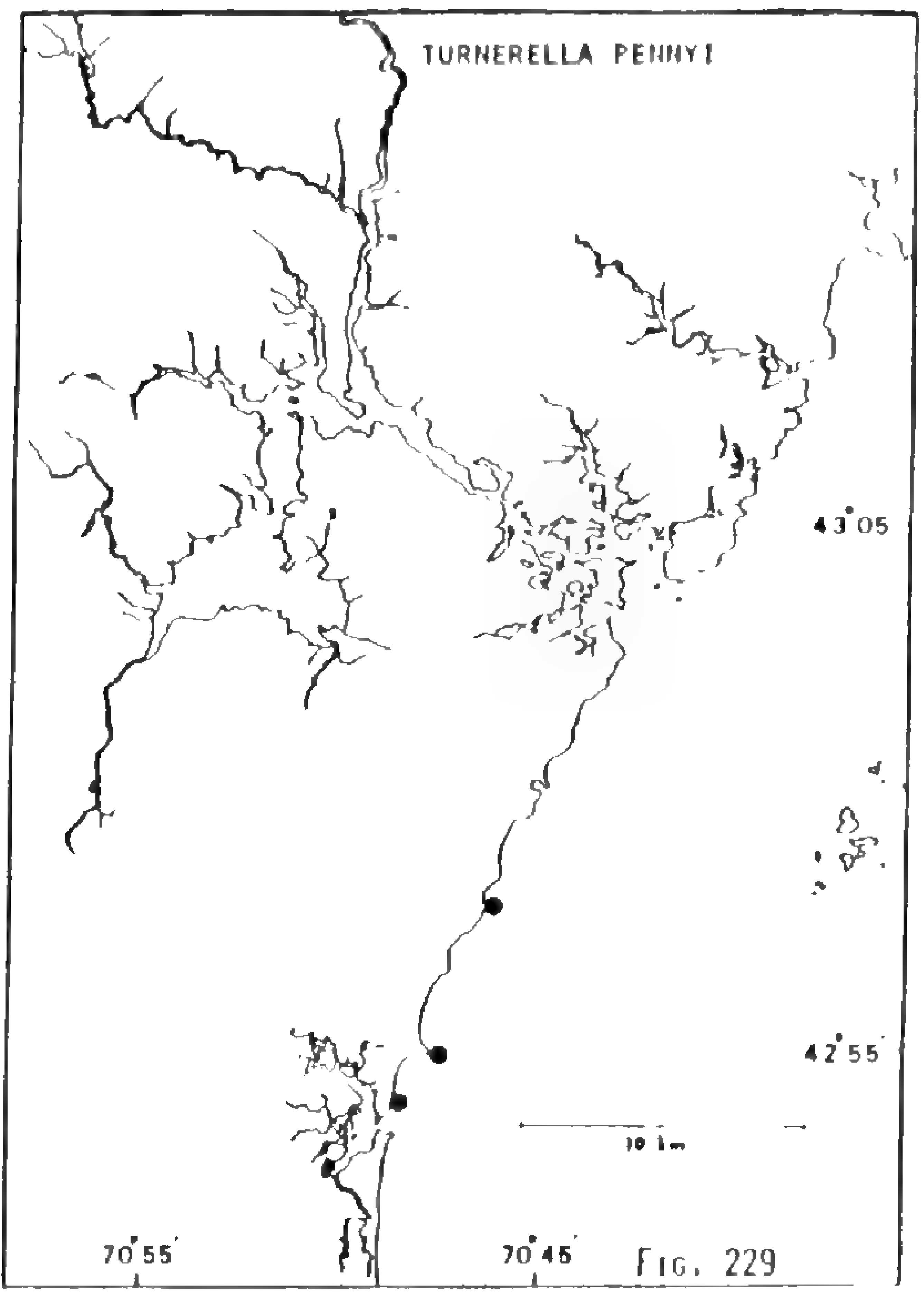


FIG. 229

APPENDIX

NEARSHORE OPEN COAST BETWEEN SOUTHERN MAINE AND NEW HAMPSHIRE

Station Number	Latitude and Longitude	Description
C1	43°12′16″N, 70°34′W	Bald Head Cliff, Ogunquit, Maine
C2	43°09′56″N, 70°35′25″W	Nubble Light, Cape Neddick, Maine
C3	43°05′26″N, 70°30′32″W	Sea Point, Maine
C4	43°03′38″N, 70°41′42″W	Kittery Point, Maine
C5	43°03′22″N, 70°42′49″W	Jaffrey Point, Fort Stark, New Hampshire
C6	43°02′15″N, 70°43′20″W	Odiorne's Point, Frost Point, Fort Dearborn, New Hampshire
C7	43°01′30″N, 70°43′20″W	Seal Rocks, New Hampshire
C8	43°01′20″N, 70°42′15″W	Gunboat Shoals, New Hampshire
C9	43°01′25″N, 70°43′40″W	North Wallis Sands, New Hampshire
C10	43°01′00″N, 70°43′55″W	Concord Point, New Hampshire
C11	43°00′05″N, 70°44′30″W	Ragged Neck, New Hampshire
C12	42°58′20″N, 70°45′33″W	Rye Ledge, New Hampshire
C13	42°57′30″N, 70°46′30″W	Little Boar's Head, New Hampshire
C14	42°57′00″N, 70°46′44″W	Godfrey's Ledge, North Hampton, New Hampshire
C15	42°55′05″N, 70°47′18″W	Great Boar's Head, New Hampshire
C16	42°54′30″N, 70°48′30″W	Hampton Beach, New Hampshire
C17	42°53′30″N, 70°48′45″W	Bound Rock, area in the immediate vicinity of Beckman's Point, near mouth of Hampton Harbor, Hampton, New Hampshire

GREAT BAY ESTUARY SYSTEM
PISCATAQUA RIVER

(New Hampshire/Maine)

Station No.	Latitude and Longitude	Miles From Coast	Description
P1	43°04′00″N, 70°41′46″W	.05	Gerrish Island, at Fort Foster, northeast of Wood Island, Kittery, Maine
P2	43°03′31″N, 70°42′58″W	.2	Wentworth Point, Little Harbor, New Castle, New Hampshire
P3	43°03′20″N, 70°43′18″W	.1	Little Harbor Estuary, point northeast of Frost Point, New Castle, New Hampshire
P4	43°03′01″N, 70°43′55″W	.85	Witch Creek, Rye, New Hampshire
P5	43°03′25″N, 70°44′20″W	1.3	Sagamore Creek, Portsmouth, New Hampshire
P6	43°03′34″N, 70°44′15″W	1.25	Goose Island, near mouth of Sagamore Creek, Portsmouth, New Hampshire
P7	43°04′20″N, 70°42′30″W	.8	Fort Constitution, Fort Point, New Castle, New Hampshire
P8	43°04′24″N, 70°42′56″W	1.4	Salamander Point, New Castle, New Hampshire
P9	43°04′19″N, 70°43′47″W	2.1	Shaw's Hill, New Castle, New Hampshire
P10	43°04′14″N, 70°43′48″W	2.1	Riverside Cemetery, New Castle, New Hampshire
P11	43°04′12″N, 70°44′26″W	2.7	Shapleigh Island, Portsmouth, New Hampshire
P12	43°04′29″N, 70°44′48″W	2.8	Pierce Island, Portsmouth, New Hampshire
P13	43°04′44″N, 70°45′12″W	3.4	Memorial Bridge and adjacent Fisherman's Pier area, also Electric Plant, Portsmouth, New Hampshire
P14	43°04′46″N, 70°45′28″W	3.6	Ceres Street, upstream from P13, Portsmouth, New Hampshire
P15	43°05′09″N, 70°45′40″W	4	Bridge at Rte. 1 bypass, west bank, Portsmouth, New Hampshire

Great Bay Estuary System/Piscataqua River (NH, ME) (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
P16	43°05′13″N, 70°45′52″W	4.3	Freeman's Point, Normandeau Schiller Site No. 12 (New Hampshire side at Maine-New Hampshire Rte. 1 bypass bridge) Portsmouth, New Hampshire
P17	43°05′26″N, 70°45′39″W	4.5	Normandeau Schiller Site No. 13 (on Maine side in creek west of Maine-New Hampshire Rte. 1 bypass bridge) end of Adams Lane, Kittery, Maine
P18	43°05′36″N, 70°46′08″W	4.7	Atlantic Heights and Normandeau Schiller Site No. 14 (west of "new" bridge New Hampshire side) Portsmouth, New Hampshire
P19	43°05′43″N, 70°46′10″W	4.9	Normandeau Schiller Site No. 15 (east of navigation point and high tension towers) Eliot, Maine
P20	43°05′52″N, 70°46′03″W	5.0	Spinney Creek, at south Eliot Road Bridge, Eliot, Maine (including Jerry's Marina)
P21	43°05′40″N, 70°46′46″W	5.0	Dock at Sprague Terminal, Portsmouth, New Hampshire
P22	43°05′41″N, 70°46′51″W	5.3	Normandeau Schiller Site No. 16 (in cove east of Schiller Generating Station) Portsmouth, New Hampshire
P23	43°05′51″N, 70°47′02″W	5.5	Schiller Station, Portsmouth, New Hampshire
P24	43°06′02″N, 70°46′52″W	5.6	Normandeau Schiller Site No. 17 and 17D (Maine side at end of Long Reach Farm) Eliot, Maine
P25	43°06′15″N, 70°47′47″W	5.6	Newington Power Station and Normandeau Schiller Sites Nos. 18-40 (between Schiller Plant and Simplex Pier; benthic stations 300′ offshore LW marsh, and 500′ from HW mark) and Normandeau Schiller

			Transects A–C, Simplex Plant–Pier, Newington, New Hampshire
P26	43°06′21″N, 70°47′49″W	6.5	Normandeau Schiller Site No. 42 (on the west side of the Simplex Pier) and Normandeau Schiller Transects D & E, Newington, New Hampshire
P27	43°06′32″N, 70°47′34″W	6.45	Normandeau Schiller Site No. 19 (one-half mile east of Frankfort Island) Park Street, Eliot, Maine
P28	43°06′38″N, 70°47′47″W	6.6	Public landing end of Green Acre Road and just upstream and opposite from Simplex Dock, Eliot, Maine
P29	43°06′28″N, 70°47′58″W	6.7	Normandeau Schiller Site No. 44 (in a large cove west of the Simplex Pier) and Union Oil Terminal, Newington, New Hampshire
P30	43°06′33″N, 70°48′13″W	6.85	Town Landing, Newington, New Hampshire
P31	43°06′44″N, 70°48′32″W	7.1	Normandeau Schiller Site No. 46 (east of old shipyard and west of Union Oil Terminal), Newington, New Hampshire
P32	43°06′53″N, 70°47′57″W	7	Mast Cove (Searles Cove) and Normandeau Schiller Site No. 21 (in Mast Cove behind Frankfort Island) Eliot, Maine
P33	43°06′52″N, 70°48′08″W	7.05	Frankfort Island, Eliot, Maine
P34	43°07′07″N, 70°48′06″W	7.4	Mast Cove (Searles Cove) and Normandeau Schiller Site No. 23 (east of Adlington Creek), Eliot, Maine
P35	43°06′58″N, 70°48′42″W	7.6	Normandeau Schiller Site No. 48 (west of Atlantic terminal), Newington, New Hampshire
P36	43°07′00″N, 70°49′24″W	8.2	Bloody Point, opposite Hilton Park and Normandeau Schiller Site No. 50 (cove on northeast side of General Sullivan Bridge), Newington, New Hampshire
P37	43°07′16″N, 70°48′22″W	7.65	North of Adlington Creek mouth, Eliot, Maine

Great Bay Estuary System/Piscataqua River (NH, ME) (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
P38	43°07′18″N, 70°48′45″W	7.8	East bank at first promontory upstream from Adlington Creek at a public dock, Eliot, Maine
P39	43°07′25″N, 70°49′02″W	7.95	East bank opposite General Sullivan Bridge and Normandeau Schiller Site No. 25 (on Maine side directly across from the eastern point of the General Sullivan Bridge) Eliot, Maine
P40	43°07′17″N, 70°49′25″W	8.2	Offshore ledge upstream from Dover Point, Dover, New Hampshire
P41	43°07′33″N, 70°50′05″W	8.9	Pomeroy Cove, Dover, New Hampshire
P42	43°07′38″N, 70°49′16″W	8.55	East bank along River Road and approximately opposite Pomeroy Cove (Hilton Park is opposite this), Eliot, Maine
P43	43°07′51″N, 70°49′21″W	8.7	Stacey Creek mouth, Eliot, Maine
P44	43°07′55″N, 70°49′25″W	8.95	East bank, first major promontory upstream of Stacey Creek, Eliot, Maine
P45	43°07′45″N, 70°49′59″W	8.95	West bank at the end of Cote Drive, Dover, New Hampshire
P46	43°08′05″N, 70°49′38″W	9.35	East bank opposite Pineview Drive ending at Rogers Pt. Road, Eliot, Maine
P47	43°08′09″N, 70°49′58″W	9.45	West bank, Pineview Drive ending, Dover, New Hampshire
P48	43°08′29″N, 70°49′48″W	9.8	East bank just southeast and opposite from the end of Roberts Road, Eliot, Maine
P49	43°08′38″N, 70°50′04″W	10	West bank at the end of Roberts Road, Dover, New Hampshire
P50	43°08′48″N, 70°49′55″W	10.1	East bank, opposite and southeast from Riverside Drive, Eliot, Maine
P51	43°09′01″N, 70°50′07″W	10.4	West bank just northeast of Riverside Drive, Dover, New Hampshire

P52	43°08′59″N, 70°49′53″W	10.45	East bank just south of Sturgeon Creek, opposite Riverside Drive, Eliot, Maine
P53	43°09′11″N, 70°49′48″W	10.7	East bank just south of mouth of Sturgeon Creek, Eliot, Maine
P54	43°09′25″N, 70°49′40″W	10.95	East bank just north of mouth of Sturgeon Creek, at Tidy Road, Eliot, Maine
P55	43°09′44″N, 70°49′54″W	11.3	Just southeast of the end of Dover Neck Road, west bank upstream from Sturgeon Creek, Dover, New Hampshire
P56	43°10′03″N, 70°49′38″W	11.7	East bank at large tennis court facility, approximately mid way between Sturgeon Creek and the mouth of the Salmon Falls River, at the end of Houde Road, Eliot, Maine
P57	43°10′16″N, 70°49′43″W	12	Northeast of Dover Neck Road, near power lines, Dover, New Hampshire
P58	43°10′19″N, 70°49′30″W	12	East bank opposite Dover Neck Road, near power lines opposite Gould Corner, Eliot, Maine
P59	43°10′25″N, 70°49′30″W	12.1	West bank just south of Cocheco River junction, Dover, New Hampshire

LITTLE BAY
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles from Coast	Description
LB1	43°07′07″N, 70°49′42″W	8.6	Dover Point, including Hilton Park and pilings at Sullivan's Bridge, Dover
LB2	40°07′17″N, 70°50′04″W	8.95	Benn's Marina, west bank of Dover Point and upstream from Hilton Park, Dover
LB3	43°06′57″N, 70°49′46″W	8.7	Point between Great Bay Marina and General Sullivan Bridge, and just

Little Bay (NH) (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
			northwest of Newington Station, Newington
LB4	43°06′56″N, 70°50′02″W	8.9	Great Bay Marina, point due west of LB3, Newington
LB5	43°06′54″N, 70°50′34″W	9.45	Broad Cove, Newington
LB6	43°07′21″N, 70°50′45″W	9.5	Submarine ledge, southeast of Goat Island, a peninsula in Little Bay, Newington
LB7	43°07′45″N, 70°51′08″W	10.2	Cedar Point including shoreline of Little Bay and Royals Cove, Durham
LB8	43°07′27″N, 70°51′19″W	10	Goat Island and adjacent rock outcrops, Newington
LB9	43°07′13″N, 70°51′47″W	11	Fox Point, Newington
LB10	43°07′14″N, 70°52′10″W	11.1	Durham Point except northwest tip along the bank of the Oyster River (01), Durham
LB11	43°06′57″N, 70°51′57″W	11.4	Langley's Island, formerly Sassafrass Island; Seal Rocks and adjacent offshore ledge, Durham
LB12	43°06′54″N, 70°52′03″W	11.45	End of Colony Cove, just south of Durham Point, Durham
LB13	43°06′23″N, 70°52′14″W	11.55	East bank of Little Bay at junction of power cable, Durham
LB14	43°05′56″N, 70°52′02″W	11.9	Stone House, east bank and south of LB13, approximately 2/3 of the distance between Adams Point to Langley's Island, Durham
LB15	43°05′51″N, 70°52′11″W	12	In front of P. Sawyer's old house, Durham
LB16	43°05′43″N, 70°52′07″W	12.25	Adams Point, Durham
LB17	43°05′47″N, 70°51′16″W	12	First promontory north of Welch Cove, Newington
LB18	43°05′41″N, 70°51′15″W	12.15	Welch Cove, Newington

LB19	43°05′35″N, 70°51′30″W	12.25	Second promontory south of Welch Cove, Newington
LB20	43°05′32″N, 70°51′44″W	12.2	Furber Strait, Durham/Newington
LB21	43°05′24″N, 70°51′39″W	12.35	Promontory due east of Adams Point, Newington

GREAT BAY
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
GB1	43°05′52″N, 70°53′52″W	13.9	Crommet Creek at Bay Road Bridge, Durham
GB2	43°05′13″N, 70°52′21″W	12.9	Footman Islands, Durham
GB3	43°05′05″N, 70°52′48″W	13.35	First major promontory southwest of Footman Island, Durham
GB4	43°04′49″N, 70°53′25″W	15	Third major promontory southwest of Footman Island, Newmarket
GB5	43°04′03″N, 70°54′25″W	15.3	Moody's Point, end of Smith Garrison Road (except for L2 just upstream from Moody's Point), Newmarket
GB6	43°03′50″N, 70°54′45″W	15.65	Shackford Point, Newmarket (except for L1, second promontory upstream on Shackford Point)
GB7	43°03′39″N, 70°54′50″W	15.8	West bank, due south of Shackford Point, near mouth of Squamscott River, Newmarket
GB8	43°03′46″N, 70°54′34″W	14.7	Sandy Point, Greenland
GB9	43°03′35″N, 70°52′17″W	14.5	Brackett's Point, Greenland
GB10	43°03′32″N, 70°51′42″W	14.65	Weeks Point, Greenland
GB11	43°03′05″N, 70°51′16″W	15.2	Point due west of Pierce Point, just beyond mouth of Winnicut River, Greenland
GB12	43°03′14″N, 70°50′48″W	15.5	Pierce Point, Greenland
GB13	43°04′05″N, 70°50′48″W	15.05	Fabyan's Point, Newington
GB14	43°04′08″N, 70°51′47″W	13.85	Nannie Island, Newington
GB15	43°04′16″N, 70°51′40″W	13.75	Woodman Point, Newington
GB16	43°04′53″N, 70°51′56″W	13	Thomas Point, Newington

BELLAMY RIVER
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
B1	43°07′47″N, 70°50′52″W	10.4	Mouth, east bank near Scammel Bridge pilings, Dover
B2	43°08′06″N, 70°50′36″W	10.75	East bank, opposite Clements' Point and near toll plaza, Dover
B3	43°08′09″N, 70°51′02″W	10.75	Clements' Point, Dover
B4	43°08′49″N, 70°50′54″W	11.6	West bank, opposite from Bellamy Lane, Dover
B5	43°09′21″N, 70°51′17″W	12.3	West and east banks at Nute Road, Dover
B6	43°09′47″N, 70°51′23″W	12.8	East bank at Cushing Road, Dover
B7	43°09′57″N, 70°51′37″W	13.1	East bank, end of Spur Road near Greek cemetery, Dover
B8	43°10′16″N, 70°51′52″W	13.5	West bank, near the end of Mast Road, Dover
B9	43°10′33″N, 70°52′20″W	14	West bank, opposite Mill Street, Dover
B10	43°10′39″N, 70°52′30″W	14.25	Headwaters, below tidal dam, near Sawyer's Mills, Dover

COCHECO RIVER
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
C1	43°10′44″N, 70°49′48″W	12.6	Mouth, on east bank and opposite peninsula separating Cocheco from Piscataqua River, Dover
C2	43°10′58″N, 70°50′09″W	13.2	West bank, just opposite and somewhat south of the end of Three Rivers Road, Dover
C3	43°11′12″N, 70°50′17″W	13.3	East bank at the mouth of Fresh Creek, Dover
C4	43°11′10″N, 70°50′27″W	13.5	West bank, just opposite mouth of Fresh Creek, Dover

C5	43° 11′44″N, 70° 50′13″W	14	Fresh Creek at Rte. 101 Bridge (Gulf Road), Dover
C6	43° 11′25″N, 70° 50′34″W	13.7	East bank, just upstream from Fresh Creek, Dover
C7	43° 11′21″N, 70° 50′48″W	13.9	East of McKone Road Landing, just downstream from lower narrows, Dover
C8	43° 11′30″N, 70° 51′01″W	14.05	Lower narrows on west bank near marsh from McKone Road Landing, Dover
C9	43° 11′30″N, 70° 51′11″W	14.25	Upstream from lower narrows, northeast of McKone Road Landing, Dover
C10	43° 11′38″N, 70° 51′11″W	14.4	East bank just east of Cocheco Country Club, opposite McKone's Marsh, Dover
C11	43° 11′44″N, 70° 51′26″W	14.6	East bank, west of Cocheco Country Club and just upstream from the mouth of Emerson Brook, Dover
C12	43° 11′46″N, 70° 51′48″W	14.7	East bank near Dover Sewage Treatment Plant and red brick factory, Dover
C13	43° 11′50″N, 70° 51′52″W	14.9	East of red brick factory, near cemetery at Cocheco Street, east bank, Dover
C14	43° 11′47″N, 70° 51′58″W	15	East of Dover sewage treatment plant, west bank, Dover
C15	43° 11′47″N, 70° 52′15″W	15.4	Northeast of Old Water Street Bridge, near George's Marina and the Davis School, Dover
C16	43° 11′40″N, 70° 52′15″W	15.5	Between the two Water Street bridges and on west bank, Dover
C17	43° 11′41″N, 70° 52′22″W	15.75	Headwaters, at Central Avenue and near the fish ladder, Dover

LAMPREY RIVER
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
L1	43°03′52″N, 70°54′53″W	15.8	Mouth, second promontory upstream on Shackford Point, Newmarket
L2	43°03′57″N, 70°54′49″W	15.75	Mouth, just upstream from Moody's Point on north bank, Newmarket
L3	43°04′07″N, 70°55′12″W	16.25	East bank opposite fish seines by private dock, Newmarket
L4	43°04′09″N, 70°55′20″W	16.4	Just beyond fish seine on west bank near Birch Drive, Newmarket
L5	43°04′19″N, 70°55′38″W	16.6	West bank in small cove between lower narrows and fish seines, Newmarket
L6	43°04′27″N, 70°55′39″W	16.75	East bank just south of lower narrows and opposite overhead power cables, and opposite the end of Young's Lane, Newmarket
L7	43°04′31″N, 70°55′47″W	16.85	West bank and southwest of overhead power cables and opposite the end of Young's Lane, Newmarket
L8	43°04′38″N, 70°56′06″W	17.25	Upper narrows, east bank, Newmarket
L9	43°04′50″N, 70°56′01″W	17.5	Headwater, near dam to Sewage Treatment Plant and at Rte. 108, Newmarket

OYSTER RIVER
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
O1	43°07′23″N, 70°52′20″W	11.5	Mouth, northwest tip of Durham Point and just north of Langley Road, Durham
O2	43°07′29″N, 70°52′17″W	11.5	Mouth, Emerson's Beach, pier area and red boat house, opposite from Durham Point, Durham

O3	43°07′32″N, 70°52′53″W	11.95	Large private dock, north of Mathes Farm Road, Durham
O4	43°07′42″N, 70°52′36″W	11.8	Smith Creek, mouth, Durham
O5	43°07′43″N, 70°52′58″W	12.25	Midway between Smith and Bunker Creeks on the Rte. 4 side, Durham
O6	43°07′58″N, 70°53′10″W	12.5	Mouth, Bunker Creek, Durham
O7	43°07′52″N, 70°53′50″W	13	Directly across from the mouth of Johnson Creek, Durham
O8	43°07′59″N, 70°53′48″W	13	Mouth, Johnson Creek, near Riverview Court ending, Durham
O9	43°08′14″N, 70°54′00″W	13.45	Johnson Creek Bridge at Rte. 4, Durham
O10	43°07′59″N, 70°54′16″W	13.35	Mouth, Horsehide Brook, Durham
O11	43°08′12″N, 70°54′27″W	13.6	Just upstream of Durham Waste Treatment Plant, Durham
O12	43°08′05″N, 70°54′40″W	13.75	Opposite Jackson's Landing, Durham
O13	43°08′05″N, 70°54′48″W	13.90	Mouth, Beards Creek, Durham
O14	43°07′52″N, 70°55′06″W	14.2	Headwater at Rte. 108, along Old Landing Road, Durham

SALMON FALLS RIVER
(New Hampshire/Maine)

Station No.	Latitude and Longitude	Miles From Coast	Description
SF1	43°10′48″N, 70°49′40″W	12.5	Mouth, on east bank of peninsula separating Piscataqua River from Salmon Falls River, Dover, N.H.
SF2	43°10′37″N, 70°49′26″W	12.6	Mouth, east bank, South Berwick, Maine
SF3	43°10′52″N, 70°49′16″W	12.7	First brook on Salmon Falls River, mouth, South Berwick, Maine
SF4	43°10′53″N, 70°49′41″W	12.8	West side, opposite the mouth of the first brook (or SF3), Dover, New Hampshire
SF5	43°11′18″N, 70°49′38″W	13.25	East bank, just south of Rte. 101 (Eliot) bridge, South Berwick, Maine

Salmon Falls River (NH) (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
SF6	43°11′23″N, 70°49′48″W	13.3	West bank, opposite and somewhat south of Rte. 101 (Eliot) Bridge, Dover, New Hampshire
SF7	43°11′24″N, 70°49′30″W	13.5	East side at Rte. 101 (Eliot) Bridge, South Berwick, Maine
SF8	43°11′25″N, 70°49′20″W	13.8	Just upstream from Rte. 101 (Eliot) Bridge, east bank at end of Waterside Lane, South Berwick, Maine
SF9	43°11′40″N, 70°48′59″W	14	East bank, by cemetery, near Rte. 101 (Eliot) Bridge, South Berwick, Maine
SF10	43°11′50″N, 70°49′06″W	14.2	Above SF9, approximately 1/3 the distance between Rte. 101 (Eliot) Bridge and Hamilton House, South Berwick, Maine
SF11	42°59′47″N, 70°56′20″W	14.8	Mouth, Sligo Brook, Rollinsford, New Hampshire
SF12	42°59′43″N, 70°51′20″W	15.2	Hamilton House near mouth of Hamilton Brook, South Berwick, Maine
SF13	43°11′59″N, 70°49′11″W	15.75	East bank, just below Leigh's Mill Pond, South Berwick, Maine
SF14	43°12′01″N, 70°49′23″W	15.75	West bank near Sligo Road and opposite SF13, Rollinsford, New Hampshire
SF15	42°51′03″N, 70°57′00″W	16.3	East bank just above Leigh's Mill Pond, South Berwick, Maine
SF16	42°58′51″N, 70°56′43″W	16.5	Headwater at Portland Avenue Bridge, east and west banks, South Berwick, Maine

SQUAMSCOTT RIVER
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
S1	43°03′09″N, 70°54′47″W	16.2	Mouth, on west bank at railroad bridge, Newfields
S2	43°02′59″N, 70°55′03″W	16.5	West bank near creek and just upstream from railroad bridge, Newfields
S3	43°02′51″N, 70°55′02″W	16.7	West bank, just upstream of S2 and midway between towers and Rte. 108 Bridge, Newfields
S4	43°02′33″N, 70°55′09″W	16.9	East bank at towers for overhead power cable, Stratham
S5	43°02′24″N, 70°55′43″W	17.45	Bridge at Rte. 108, Chapman's Landing, Newfields
S6	43°02′01″N, 70°56′13″W	18	East bank, upstream of Chapman's Landing and 1/4 of the way between S5 and S9, Newfields
S7	43°01′35″N, 70°56′04″W	18.55	East bank, halfway between S5 and S9, Stratham
S8	43°01′11″N, 70°55′57″W	19.2	East bank near private dock and three quarters of the way between S5 and S9, Stratham
S9	43°00′46″N, 70°56′23″W	19.75	West bank by railroad track, near overhead power lines (towers), Exeter
S10	43°00′01″N, 70°56′24″W	20.75	West bank, just upstream of oxbow cut and just north of Rte. 101 fixed bridge, Exeter
S11	42°59′48″N, 70°56′19″W	21	Opposite the mouth of Wheelwright Creek, Exeter
S12	42°59′43″N, 70°56′20″W	21.2	East bank, just upstream from the mouth of Wheelwright Creek, Exeter
S13	42°59′31″N, 70°56′42″W	21.5	West bank just upstream from Powell's Point, Exeter
S14	42°59′17″N, 70°57′03″W	21.9	West bank by dike and water outfall, also near the mouth of Norris Brook, Exeter

Squamscott River (NH) (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
S15	42°59′03″N, 70°57′01″W	22.25	Just upstream and opposite Powderhouse Point, Exeter
S16	42°58′52″N, 70°56′41″W	22.7	Headwaters at tidal dam, Exeter

WINNICUT RIVER
(New Hampshire)

Station No.	Latitude and Longitude	Miles From Coast	Description
W1	43°02′47″N, 70°50′40″W	15.8	Mouth, on west bank and near the mouth of Shaw Brook, across from Portsmouth Country Club, Greenland
W2	43°02′52″N, 70°50′16″W	16.25	Mouth, on east bank and downstream from Packer's Brook, a cove area, Greenland
W3	43°02′31″N, 70°50′28″W	16.75	East bank just downstream from railroad bridge and near the end of Tide Mill Road, Greenland
W4	43°02′12″N, 70°50′55″W	17.25	Headwaters at the Rte. 101 (Portsmouth Avenue) Bridge, Greenland

HAMPTON-SEABROOK ESTUARY
(New Hampshire)
HAMPTON RIVER AND ADJACENT TRIBUTARIES

Station No.	Latitude and Longitude	Miles From Coast	Description
A-1	42°51′46″N, 70°47′02″W	1.3	At the mouth of the first major tributary SE of Tide Mill Creek on the Hampton River, Hampton

A-2	42°54′40″N, 70°49′06″W	1.91	The northeast portion of an "island" formed at the mouth of the Taylor River, Blind Creek and the upper part of Hampton River, Hampton Falls, Hampton
A-3	42°54′48″N, 70°49′40″W	1.3	Approximately 1500 feet NE of mouth of Tide Mill Creek and the Hampton River, Hampton
A-4	42°54′49″N, 70°50′04″W	2.3	Approximately 1800 feet NW of station A-2 on the Hampton River, Hampton Falls, Hampton
A-5	42°55′04″N, 70°50′32″W	3.3	Opposite a small brook, which empties into the first tributary above the mouth of Hampton Falls River, Hampton
A-6	42°55′19″N, 70°50′10″W	3.2	At the junction of the first oxbow NE of Station A-5 on the Taylor River, Hampton
A-7	42°55′34″N, 70°50′30″W	3.1	Hampton Landing on Taylor River, Hampton
A-8	42°55′12″N, 70°50′08″W	2.31	At the mouth of Nudds Canal and Blink Creek, Hampton
A-9	42°55′24″N, 70°49′08″W	2.56	Tide Mill Creek by the Route 101 bridge, Hampton
A-10	42°54′47″N, 70°51′18″W	5.2	Hampton Falls River south of Depot Avenue and near the Boston and Maine Railroad bridge, Hampton Falls
A-11	42°55′40″N, 70°50′38″W	4.4	A site approximately 2000 feet SW of the Boston and Maine substation, which is between Lafayette and Landing Roads. Adjacent to the Boston and Maine railroad tracks; it is on Taylor River in Hampton
A-12	42°54′39″N, 70°51′16″W	5.0	End of Depot Avenue on Hampton Falls River, Hampton Falls
A-13	42°54′58″N, 70°50′48″W	3.0	Middle of the southernmost oxbow near the mouth of Taylor River and the Hampton town line
A-14	42°55′12″N, 70°50′42″W	3.7	A bend in the first tributary above (north) of Hampton Falls River where the river crosses the

Hampton-Seabrook Est./Hampton R. & Adj. Trib. (NH) (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
			railroad tracks. Collections were made on the harbor side of the tracks, Hampton
A-15	42°55′12″N, 70°51′04″W	3.7	Same as A-14, except the land side of the railroad tracks, Hampton
A-16	42°55′13″N, 70°50′42″W	3.5	A salt marsh on a point of land made by the Hampton River and the first tributary above the Hampton Falls River, between stations A-5 and A-14, Hampton
A-17	42°55′20″N, 70°49′54″W	3.01	Hampton Landing, Taylor River, Hampton
A-18	42°54′34″N, 70°49′24″W	1.6	The Willows—at the mouth of Tide Mill Creek and Hampton River, Hampton

BROWN RIVER AND ADJACENT TRIBUTARIES

Station No.	Latitude and Longitude	Miles From Coast	Description
B-1	42°53′55″N, 70°49′06″W	1.0	A small "island" opposite Eastman's Slough and about 2500 feet west of the Locke Point State Park area
B-2	42°53′45″N, 70°50′14″W	1.7	Southernmost portion of Eastman Slough, near Halftide Rock and at the mouth of the Brown River, Hampton Falls-Seabrook
B-3	42°53′40″N, 70°50′40″W	1.8	Just inside the mouth of Hunt's Island Creek at the junction of Brown River (on the east side of the channel). Approximately 600 feet SW of B-2, Seabrook
B-4	42°53′59″N, 70°50′28″W	2.0	Approximately 500 feet NW of the first tributary past Hunt's Island Creek, Hampton Falls-Seabrook

B-5	42°54′11″N, 70°50′18″W	2.2	Approximately 700 feet NE of the mouth of Swain's Creek, Hampton Falls
B-6	42°54′17″N, 70°50′02″W	2.3	Robbins Point, Hampton Flats, Hampton Falls-Seabrook
B-7	42°54′16″N, 70°50′14″W	2.5	Brown's River, first tributary upstream from Swain's Creek, Hampton Falls
B-8	42°53′59″N, 70°50′18″W	2.4	Approximately 800 feet upstream from Robbin's Point, Hampton Falls-Seabrook
B-9	42°54′08″N, 70°50′24″W	2.53	Approximately 700 feet upstream from Station B-8, Hampton Falls-Seabrook
B-10	42°54′07″N, 70°50′42″W	2.8	End of Rock's Road on the Brown's River, Hampton Falls-Seabrook
B-11	42°54′23″N, 70°50′46″W	3.0	Near the mouth of the first major tributary east of the head waters of Brown's River, Hampton Falls-Seabrook
B-12	42°54′14″N, 70°51′10″W	3.3	Approximately 1500 feet upstream (west) from Station B-11, just before a major oxbow, Hampton Falls-Seabrook
B-13	42°54′26″N, 70°49′08″W	2.6	Swain's Creek, neck of first oxbow, Hampton Flats, Hampton Falls

BLACKWATER RIVER AND ADJACENT TRIBUTARIES

Station No.	Latitude and Longitude	Miles From Coast	Description
C-1	42°53′12″N, 70°49′32″W	1.5	Mouth of the Blackwater River near the first tributary SW of Mills Point, Seabrook
C-2	42°52′19″N, 70°50′28″W	2.2	Approximately 1200 feet SW of the first tributary past Riverside, Seabrook
C-3	42°52′12″N, 70°50′08″W	2.3	Approximately 1200 feet south of C-2, Seabrook

Blackwater & Adjacent Tributaries (Cont.)

Station No.	Latitude and Longitude	Miles From Coast	Description
C-4	42°52′30″N, 70°49′24″W	2.4	Approximately 500 feet SE of C-3, Seabrook
C-5	42°52′55″N, 70°49′34″W	2.5	Approximately 800 feet SE of C-4, Seabrook
C-6	42°52′32″N, 70°49′18″W	2.7	Approximately 800 feet SE of C-5, near the first major tributary SE of C-2, Seabrook
C-7	42°52′28″N, 70°49′12″W	3.0	Approximately 1200 feet SE of C-6 near a large white rock
C-8	42°52′21″N, 70°49′08″W	3.3	Approximately 1500 feet SE of C-7, Seabrook
C-9	42°52′12″N, 70°49′02″W	3.6	By the route 268 bridge that crosses the Blackwater River, Seabrook
C-10	42°53′10″N, 70°49′24″W	1.3	Mill's Point at the mouth of Blackwater River, Seabrook
C-11	42°53′02″N, 70°49′44″W	1.7	Riverside, Seabrook

KNOWLES ISLAND AND MILL CREEK AREAS

Station No.	Latitude and Longitude	Miles From Coast	Description
D-1	42°53′42″N, 70°49′52″W	1.34	Mouth of Creek, between Knowles Island and mainland, Seabrook
D-2	42°53′42″N, 70°50′22″W	1.6	Before the first bend, near D-1, Seabrook
D-3	42°53′45″N, 70°50′34″W	2.1	Walton Landing at the end of Walton Road, Seabrook

HAMPTON HARBOR
(NEW HAMPSHIRE)

Station No.	Latitude and Longitude	Miles From Coast	Description
H-1	42°53′40″N, 70°49′18″W	0.4	Hampton Harbor at the junction of the middle piling of the tall bridge and the tower at Hampton
H-2	42°53′20″N, 70°49′24″W	1.0	Hampton Harbor, in the channel near the mouth of the Blackwater River and at the junction of the imaginary line between Seabrook Marina and Knowles Island, Hampton
H-3	42°53′55″N, 70°48′58″W	0.8	Hampton Harbor, Smith and Gilmore Marina, Hampton
H-4	42°54′05″N, 70°49′12″W	0.97	Hampton Harbor, Hampton Marina at the mouth of Hampton River, Hampton. The station was the point protruding into the harbor proper.

CYTOLOGY OF *CAREX PURPURIFERA* MACK. (CYPERACEAE)[1]

JAMES R. MANHART

ABSTRACT

Field work and morphological studies on section Laxiflorae Kunth of the genus *Carex* L. revealed morphological variation in *C. purpurifera* Mack. is correlated with geographical distribution. *Carex purpurifera* appears to consist of two taxa, one found on soils derived from limestone in the western part of the range and the other on non-limestone-derived soils in the eastern part of the range. Morphological differences were retained in greenhouse-grown plants. Pollen mother cell counts of the western populations were $n = 17$, 18, and 19. The eastern populations were $n = 14$ only, the lowest recorded in section Laxiflorae. These cytological data support the contention that *C. purpurifera* consists of two distinct taxa and the newer one, *C. manhartii* Bryson, has been described elsewhere as a species.

Key Words: Cytology, *Carex purpurifera*, section Laxiflorae, Cyperaceae

Cytological studies of the genus *Carex* L. have long been a source of considerable confusion and speculation. Members of the genus *Carex* exhibit remarkable variation regarding chromosome numbers. In North American *Carex*, haploid numbers range from 6 to 56 with every number from 12 through 43 represented (Wahl, 1940). There is also a great deal of intraspecific variation; Tanaka (1949) pointed out that two to as many as six different chromosome numbers have been found in 70 different species.

Polyploidy is thought to be unimportant in the evolution of the genus *Carex* (Heilborn, 1924). Agmatoploidy, a special type of aneuploidy resulting from chromosome fragmentation coupled with unlocalized centromeres, is considered the major cause of speciation in *Carex* (Davies, 1956). In organisms with localized centromeres, breakage of the chromosomes usually results in the loss of the non-centromere-containing fragment. However, when unlocalized centromeres are present, the fragments can be perpetuated and become permanent components. Agmatoploidy then provides an explanation for the fact that within an aneuploid series the taxa which have the higher chromosome numbers have smaller chromosomes.

---

[1] Based on a dissertation submitted by the author to the Graduate School, University of Georgia, in partial fulfillment of the requirements for the Ph.D. degree.

Faulkner (1972) showed that in section Acutae Fries., variation within species is mainly aneuploid and that "there seems to be a remarkable instability of chromosome numbers within species of *Carex*." This variation is structural, not quantitative, and probably arises by chromosome fission and fusion due to unlocalized centromeres (Faulkner, 1972). The occurrence of agmatoploidy in *Carex* has not been unequivocally demonstrated, as Grant (1981) pointed out; however, the chromosome behavior of *Carex* closely resembles that of organisms in which unlocalized centromeres have been more clearly demonstrated (Faulkner, 1972).

Carex purpurifera Mack. was originally described and placed in section Laxiflorae Kunth by Mackenzie (1931–35) in his revision of North American *Carex*. Gleason (1952) treated *C. purpurifera* and six other taxa of section Laxiflorae as varieties of *C. laxiflora* Lam., while Bryson (Ph.D. thesis, Mississippi State Univ., 1980), in a revision of section Laxiflorae, retained all these taxa as distinct species, including *C. purpurifera*. Bryson gave a more detailed description of the distribution of *C. purpurifera* since Mackenzie (1931 35) had only seen plants from the type locality of Campbell Co., TN and one other site in Tennessee. *Carex purpurifera* is mainly found in soils which overlay limestone in dry to mesic woods along steep slopes in the southern Appalachian and Cumberland Plateau from West Virginia and eastern Kentucky south into Alabama, Georgia, North Carolina, and South Carolina (Bryson, Ph.D. thesis, Mississippi State Univ., 1980). Bryson pointed out that specimens of *C. purpurifera* from south and east of the Appalachian Divide in Georgia, North Carolina, and South Carolina have narrower leaves and less purple coloration on the leaf bases. During the course of this investigation, it was noted that plants from western populations are more robust, have glaucous leaves and long-pedunculate staminate spikes, whereas leaves of plants from eastern populations (in a very limited area without limestone underlying the soils) are not glaucous and the staminate spikes are short-pedunculate or sessile. These morphological differences are retained in greenhouse-grown plants.

Of further note, Radford et al. (1968) stated that *Carex gracilescens* Steud. is similar to *C. purpurifera*. This observation is especially true of the eastern plants, which would be the only ones occurring in North Carolina and South Carolina. However, the western plants are quite distinct from *C. gracilescens,* as this taxon has narrow, non-glaucous leaves with relatively less purple coloration on the leaf bases and a more crowded pistillate spike.

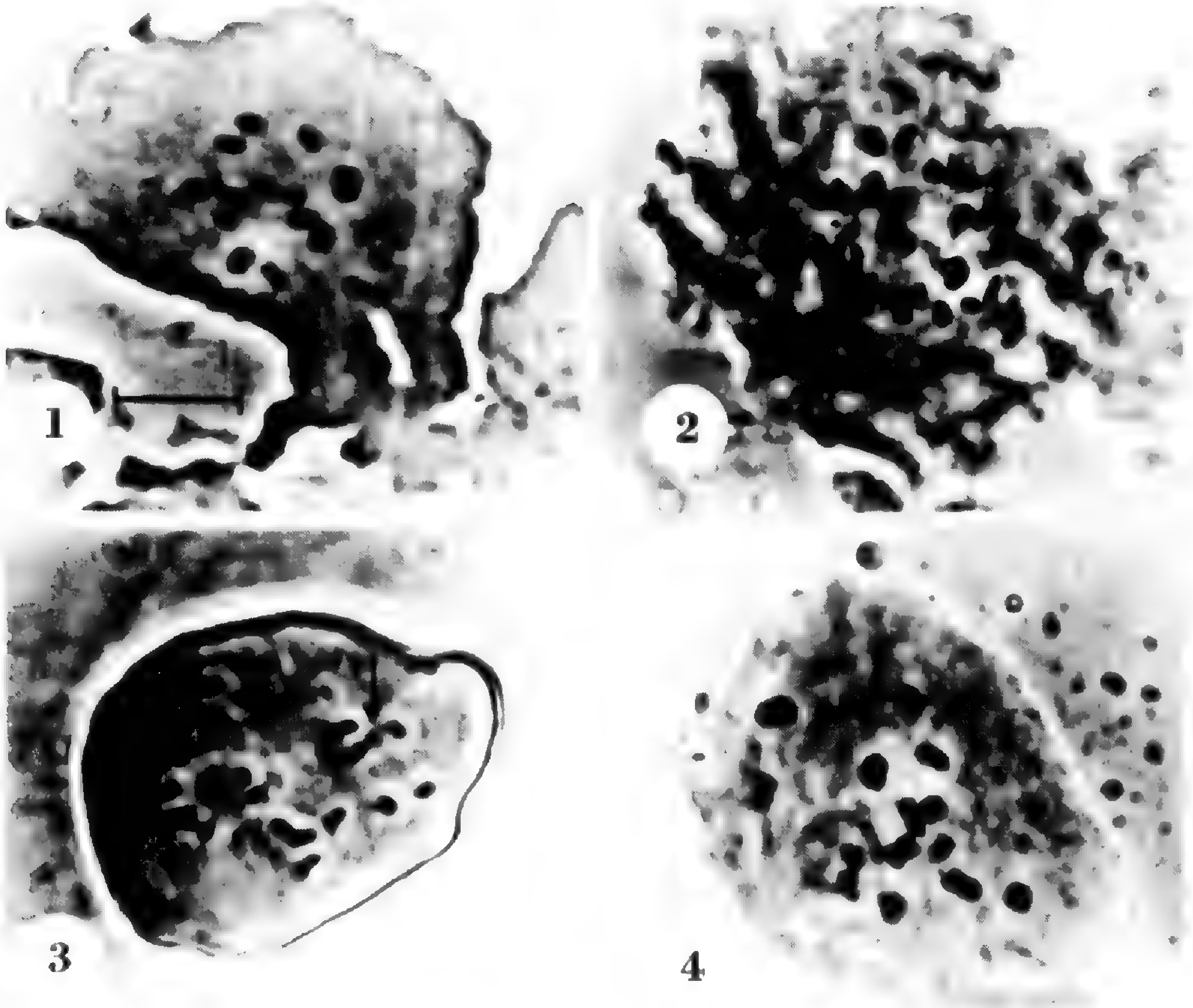
A cytological study of *Carex purpurifera* was undertaken for four reasons: (1) to determine chromosome counts for *C. purpurifera* since there are none in the literature; (2) to determine if there is a correlation of chromosome numbers with the morphological and habitat differences found between the western and eastern populations; (3) to determine if differences in chromosome numbers occur in plants from morphologically similar populations and; (4) to allow comparison of the chromosome numbers for the eastern populations of *C. purpurifera* with the three counts of $n = 20$ obtained for *C. gracilescens* by Wahl (1940).

MATERIALS AND METHODS

Meiotic counts were obtained from staminate spikes taken from plants grown in the University of Georgia Botany Department greenhouse complex and preserved in a solution consisting of chloroform:acetic acid:methanol (4:3:1 v/v). Anther squash preparations were stained with 1% aceto-carmine (Jones and Luchsinger, 1979) and photographs made of the chromosome complements (Figures 1–4). Results are based on observations of 3 to 8 cells for each preparation. Vouchers, each with a drawing and/or a photo of a countable figure, have been placed in the University of Georgia Herbarium (GA).

RESULTS AND DISCUSSION

Populations A, B, and C are from northwestern Georgia; populations B and C are 8 km from each other (Figure 5). Population D is located in Alabama 100 km west of the Georgia populations. All of these populations occur in soils with underlying limestone and the plants have wide, glaucous leaves with deep purple leaf bases and long-pedunculate staminate spikes. Population E from Macon Co., NC (Figure 5) occurs on soil with no underlying limestone as does population F which is from northeastern Georgia. Plants from populations E and F all have narrow non-glaucous leaves, with relatively less purple coloring on the leaf bases and sessile or short-pedunculate staminate spikes.



Figures 1–4. Pollen mother cells (PMC's) of *Carex purpurifera* populations. Scale = 5 micrometers. **1**. A. $n = 19$, **2**. C. $n = 17$, **3**. D. $n = 18$ (arrow indicates location of chromosome out of focal plane), **4**. E. $n = 14$

As with other taxa in the genus *Carex*, there is considerable chromosome variation in *C. purpurifera*. Meiotic counts for the four western populations vary from $n = 17$ to $n = 19$ (Table 1), numbers which are within the range for other taxa in the *C. laxiflora* complex (Wahl, 1940; Whitkus, 1981). The $n = 14$ count (Table 1) is the only one recorded for the eastern populations and is the lowest ever recorded in section Laxiflorae. Thus, the morphological and distributional differences between the western and eastern taxa are correlated with differences in the range of chromosome numbers found in these taxa.

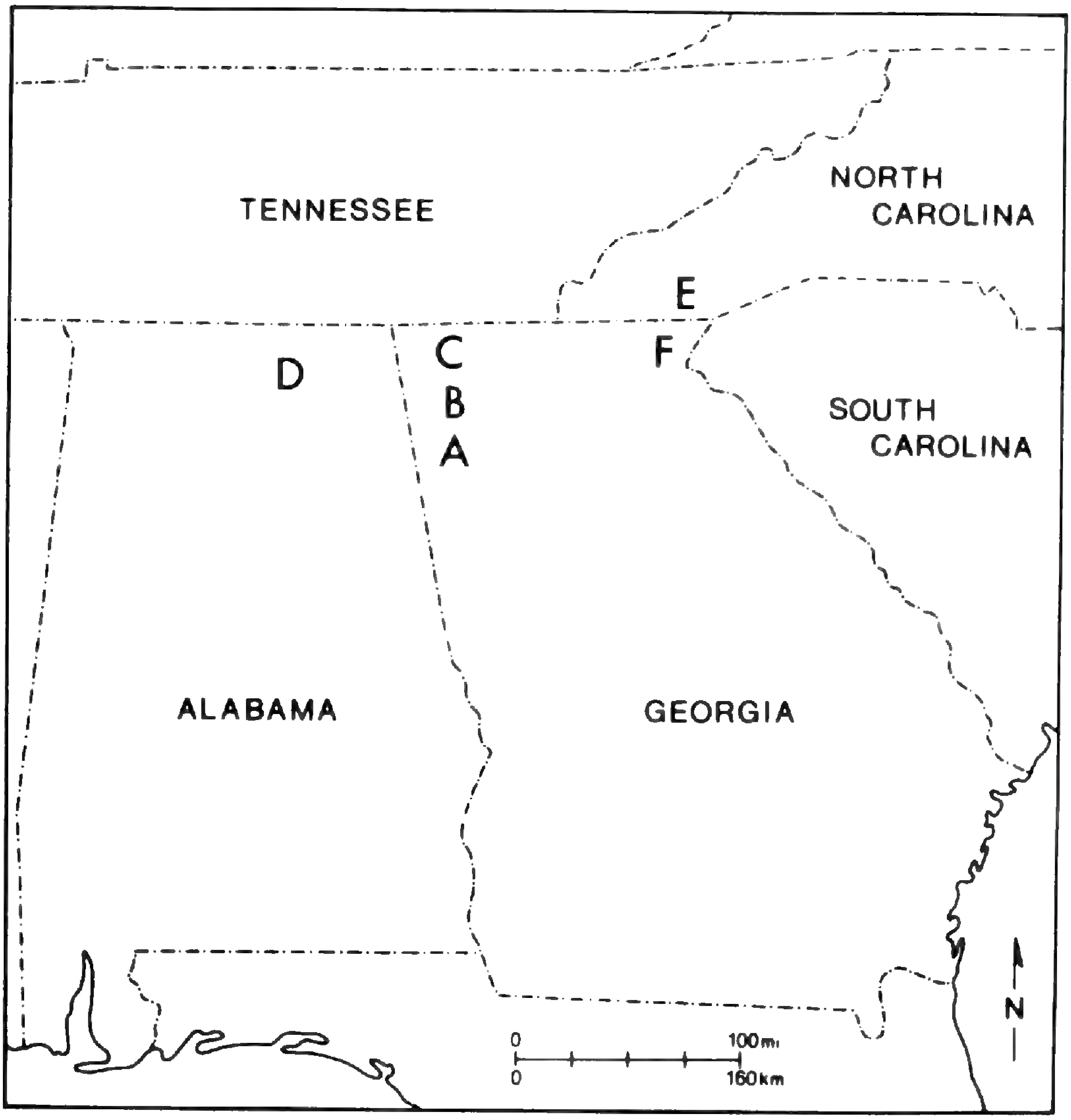


Figure 5. Locations of populations of *Carex purpurifera* sampled for cytological study.

CONCLUSIONS

The cytological data obtained in this study, in conjunction with morphological and habitat considerations, indicate that *Carex purpurifera* consists of two distinct taxa and also demonstrate that chromosome data can be quite useful in solving taxonomic problems in the genus *Carex*. In terms of the taxonomic treatment of the two taxa, Bryson (1985) has designated the eastern taxon as *C. manhartii* Bryson, a new species distinct from *C. purpurifera*.

Table 1. Meiotic Chromosome Counts (n) of *Carex purpurifera*

Population	n	Figure	Locality and Voucher
A	19	1	Floyd Co., GA, east bank of Coosa River on south side of Rome, *Manhart 378*
B	18		Walker Co., GA, Pigeon Mountain Wildlife Management Area west of Lafayette and south of GA 93, *Manhart 375*
C	17	2	Walker Co., GA, 8 km northwest of Lafayette, *Manhart 377*
D	18	3	Madison Co., AL, Monte Sano Mountain east of Huntsville, *Bryson and Manhart 3156*
E	14	4	Macon Co., NC, The Stewart Trail, Coweeta Hydrologic Laboratory, *Manhart 293*
F	14		Union Co., GA, Woods along Chattahoochee River 1 km north of Union Co.-White Co. line, *Manhart 496*

There is not enough known about speciation in *Carex* to postulate solely on chromosome numbers which of these two taxa is the "ancestral" or "most primitive" type. If it is accepted that speciation via agmatoploidy does occur in *Carex,* it is still not clear whether fission or fusion or both are involved in this process; Faulkner (1972) cited instances in which both may be involved in section Acutae. If the fission hypothesis is invoked, then the eastern taxon would have given rise to the western taxon and/or *C. gracilescens* $n = 20$; Wahl, 1940). Of course, the converse would be true if one accepts fusion as the mode of chromosomal evolution. There is simply not enough known at the present time to make a prudent choice. Further studies which incorporate morphological, chemical, distributional, and cytological data for all of section Laxiflorae should help to shed some light on speciation processes in *Carex*.

ACKNOWLEDGMENTS

I thank Nanette M. Manhart for map preparation and darkroom work, Gerald L. Smith for advice on chromosome figure interpretation, Charles T. Bryson for many helpful discussions on section Laxiflorae, David E. Giannasi for critical review of the manuscript and the University of Georgia Herbarium (GA) for technical support. This work was supported by a grant from the Botany Department at the University of Georgia, a Grant-in-Aid of Research from Sigma Xi, and NSF Pre-Doctoral Dissertation Improvement Grant DEB-8105474.

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DEPARTMENT OF BOTANY
UNIVERSITY OF GEORGIA
ATHENS, GEORGIA 30602

BOOK REVIEW

CHARLES W. JOHNSON. *Bogs of the Northeast,* Pp. 269 + xiv, tab 76. University Press of New England, Hanover, N.H. (1985) $12.95 paper; $25.00 cloth.

Bogs have always intrigued man—from earliest times as places of mysterious spirits and happenings; in modern periods as unusually interesting environmental curiosities.

The author, Vermont State Naturalist, is well qualified to write a volume on New England bogs, for he has spent a lifetime in the fields and forests of this part of the country. To the best of my knowledge, this book is the first popular but scientifically sound publication on these often misunderstood ecological peculiarities that many developers, political officials and other uninformed citizens frequently want to destroy.

The volume is divided into 17 chapters: 1) Perception of Bogs, 2) Basic Terms & Definitions, 3) Genesis of Peatlands, 4) Ferns & Bogs, 5) Geography of Northeastern Peatlands, 6) Plants & Animals, 7) Sphagnum Moss, 8) Carnivorous Plants, 9) Orchids, 10) Sedges & Heaths, 11) Insects & other Invertebrates, 12) Fish, Amphibians, Reptiles, 13) Birds, 14) Mammals, 15) Vaults of History, 16) Human Uses of Peatlands, and 17) Preservation or Obliteration? There follow a Bibliography of 117 entries, four appendices (peatlands, amphibians and reptiles, birds, mammals) and a highly detailed index.

This book is a definite contribution to New England botany.

RICHARD EVANS SCHULTES
BOTANICAL MUSEUM
HARVARD UNIVERSITY
OXFORD STREET
CAMBRIDGE, MA 02138

BOOK REVIEW

D'Arcy, William G. and Mireya D. Correa A., Editors. 1985. *The Botany and Natural History of Panama: La Botánica e Historia Natural de Panamá.* Monographs in Systematic Botany, Vol. 10, Missouri Botanical Garden. 455 pp. Dept. 11, Missouri Botanical Garden, Box 299, St. Louis, MO 63166-0299 ($48.00 plus 4% shipping charges)

This paperback book is the product of a symposium held in Panama April 14–17, 1980, to commemorate completion of the Flora of Panama, a project of long duration by many workers and collaborators at MBG. Its most striking feature is interspersal of Spanish summary paragraphs in English-language articles and English summary paragraphs in the Spanish-language articles. The reader is thus able to jump easily from one language to the other on nearly every page; the effect is that of a bilingual truly collaborative effort by specialists in the two cultures. One of my colleagues at Tufts checked the Spanish for content and readability, and ranked it first-class. Extensive literature citations are found with each article.

The text first presents data on Panama and a list of 55 author's addresses followed by papers in three groups: Part I—The Organisms, subdivided into Plant Groups, Animal Groups, Plants and Geography, and Plant Study Techniques; Part II—The Interactions of Plants, Animals and Habitats; Part III—The Human Aspect, subdivided into Plants that Affect Man, Indigenous Peoples, and Modern Man and the Landscape. Under each, a distinguished galaxy of contemporary specialists present and summarize aspects of their original work in Panama. The accounts are for the most part fascinating, perhaps more so for me because I was a member of a few of the parties doing the field work described. It is therefore possible for this reviewer to vouch firsthand for the authenticity of some of the work. Topics covered range from a history of plant collecting in Panama through ecological, evolutionary and behavioral studies of particularly prominent groups of plants and animals, from uses and abuses by people of the Panamanian tropical forests, to a genuine concern for conservation of the natural resources of Panama on the part of some Panamanians, and ending with the saddening and sobering final observation that as yet really effective conservation policies have not become a priority of the central government.

This volume is an intriguing history of thirty years of concentrated field effort which in every instance has an ongoing component still pursued by most of the same authors who wrote these papers. The flora is not yet completely tabulated, profound changes in land use are daily altering its bases and its chances of survival, and there is developing in Panamanians an even greater sense of urgency to preserve what is left of these magnificent tropical forests.

Anyone interested in the future of Central America, or who is working in any branch of its natural history, will find this volume a rich source of Panamanian cultural history, present technical problems, and ongoing directions for future conservation and research activities.

NORTON H. NICKERSON
DEPARTMENT OF BIOLOGY
TUFTS UNIVERSITY
MEDFORD, MA 02155

IN MEMORIAM

BERNARD BOIVIN 1916–1985

The following tribute to one of our former members, Bernard Boivin, appeared in The Plant Press for September 1985 (Vol. 3., No. 3).

On 9 May 1985 Canada lost one of its most productive botanists, Bernard Boivin. Born and raised in Montreal, he developed an interest in botany through his undergraduate education at the University of Montreal and the influence of Quebec botanists, especially Frère Marie-Victorin. He obtained a doctorate under Fernald at Harvard University in 1943. Although most of his career was at the Biosystematics Research Institute of Agriculture Canada in Ottawa, Dr. Boivin spent a number of years as a researcher at the Gray Herbarium of Harvard University, the National Museums of Canada, and the University of Toronto. For several years he was a researcher and lecturer at Laval University, where he continued to work until shortly before his death.

A self-described herbarium botanist, Bernard Boivin literally worked day and night on his many projects. He was the author of more than 150 publications; the best known include "Enumeration of the Plants of Canada," "Flora of the Prairie Provinces," and "Survey of Canadian Herbaria." He had completed a number of as-yet-unpublished manuscripts, the most recent on *Carex* of eastern Canada. Bernard Boivin published more names of plants, many of them new combinations, than any other Canadian botanist. Students of systematics will miss Dr. Boivin's lively discussions about aspects of taxonomy and nomenclature. Even when he might disagree on these matters, he was always good-humored and interested in their work.

Bernard Boivin believed that learning about plants is an important part of a good education for all Canadians. Realizing the value of adequate herbarium material for research, he encouraged anyone interested in plants to collect specimens. Many amateur botanists in Ontario, and the rest of Canada, were inspired by Dr. Boivin's encouragement and as a result they have made significant contributions to our knowledge of field botany. Dr. Boivin maintained extensive files for his "Index of Canadian Plant Collectors." In addition to corresponding with hundreds of individuals whose names appear on herbarium labels, he accumulated copious biographical information from newspapers and other documents. All of this material, which will be of great value to historians, is to be kept at the Hunt Institute for Botanical Documentation in Pittsburgh, Pennsylvania.

LAURENCE EATON RICHARDSON 1893–1985

The Concord Journal for Thursday, October 3, 1985 carried a notice of the death of one of our long-time members, Laurence E. Richardson, which we quote in part:

> Lawrence Eaton Richardson, 91, of Barrett's Mill Road, a Concord historian and a lifelong resident, died Thursday Sept. 26, 1985 in Acton. Born in Concord on December 10, 1893, he was the son of the late Henry Preston Richardson and the late Maria (Smith) Richardson. After attending Concord schools, he graduated from Concord High School in 1912 and from Harvard College in 1916.
>
> Mr. Richardson served as a captain with the military police of the U.S. Army during World War I. During World War II Mr. Richardson served as a Second Lt. with the 101st Field Artillery in France.
>
> For many years he was supervisor of the E & F Paint Co. in Boston. He served on the Town of Concord Finance Committee and was a member of the Concord Independent Battery, the Concord Players, and the New England Botanical Club.
>
> A well known authority on Concord history, he was the author of *Concord River* (1964) and *The Concord Independent Battery* (1973) and also other historical papers including a notable paper on the history of Concord Junction.

HESLER VISITING PROFESSORSHIPS OF FLORISTIC BOTANY

Under the terms of an endowment from Dr. and Mrs. L. R. Hesler, the Botany Department of the University of Tennessee is able to support a limited number of visiting professors of floristic botany. Stipends will be awarded based on research proposals, and may be used for salary and expenses of floristic, revisionary, or monographic systematic research. All applicants must hold faculty (or equivalent) status at a recognized botanical or educational institution. Stipend amounts and residence periods will vary, and concurrent support from the applicant's institution is strongly encouraged. Preliminary correspondence with specific departmental faculty is invited or general inquiries may be sent to:

Hesler Endowment Fund
Department of Botany
The University of Tennessee
Knoxville, TN 37996-1100 USA

THE 1985 JESSE M. GREENMAN AWARD

The Greenman Award, a cash prize of $250, is presented each year by the Missouri Botanical Garden. It recognizes the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the *previous* year. Papers published during *1985* are now being considered for the 18th annual award, which will be presented in the summer of 1986. Reprints of such papers should be sent to:

Greenman Award Committee
Department of Botany
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1986 award, reprints must be received by 1 July 1986.

NEBC 1986 AWARD
FOR THE SUPPORT OF BOTANICAL RESEARCH IN NEW ENGLAND, U.S.A.

The New England Botanical Club will again offer an award of $1,000 in support of botanical research to be conducted in the New England region during 1986. This award is being made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora,* the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double spaced pages, a budget (the budget will not affect the amount of the award), and their curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1986 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138.

The recipient of the award will be notified by 30 April 1986.

MEETING ANNOUNCEMENT AND CALL FOR ABSTRACTS

New England Graduate Student Botany Meeting

The first New England Graduate Student Botany Meeting will be held in the auditorium (Rm 153) of the Torrey Life Science Building, Department of Ecology and Evolutionary Biology, The University of Connecticut, Storrs, CT on Saturday 22 March 1986. Attendance is open to all. Paper presentations will be largely restricted to graduate student research (completed or in progress) representing all areas of botany (systematics, ecology, reproductive biology, anatomy, physiology, etc.). Time slots for paper presentations are limited and prior registration is required. Abstracts are due by 15 Feb. 1986.

For additional information and abstract forms contact:

C. Thomas Philbrick
Department of Ecology and
Evolutionary Biology, U-43
The University of Connecticut
Storrs, CT 06268
(203) 486-4156, 486-4322

or

Debra A. Dunlop
Department of Botany and
Plant Pathology
The University of
New Hampshire
Durham, NH 03824
(603) 862-3531

Vol. 87, No. 852, including pages 449 616, was issued October 28, 1985

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

Submission of a manuscript implies it is not being considered for publication simultaneously elsewhere, either in whole or in part.

Manuscripts should be submitted in **triplicate** (an original and two xerographic copies) and *must be double-spaced* (at least 3/8″) **throughout** including tables, figure legends, and literature citations. Please do not use corrasable bond. The list of legends for figures and maps should be provided on a separate page. Footnotes should be used sparingly. Do not indicate the style of type through the use of capitals or underscoring, particularly in the citation of specimens. Names of genera and species may be underlined to indicate italics in discussions. Specimen citations should be selected critically, especially for common species of broad distribution. Systematic revisions and similar papers should be prepared in the format of "A Monograph of the Genus Malvastrum", S. R. Hill, Rhodora 84: 1–83, 159–264, 317–409, 1982, particularly with reference to indentation of keys and synonyms. Designation of a new taxon should carry a **Latin diagnosis** (rather than a full Latin description), which sets forth succinctly just how the new taxon is distinguished from its congeners. Papers of a floristic nature should follow, as far as possible, the format of "Annotated list of the ferns and fern allies of Arkansas", W. Carl Taylor and Delzie Demaree, Rhodora 81: 503–548, 1979. For bibliographic citations, refer to the Botanico-Periodicum-Huntianum (B-P-H, 1968), which provides standardized abbreviations for journals originating before 1966. All abbreviations in the text should be followed by a period, except those for standard units of measure and direction (compass points). For standard abbreviations and for guidance in other matters of biological writing style, consult the *CBE Style Manual,* 5th ed. (original title: *Style Manual for Biological Journals*). In preparing figures (maps, charts, drawings, photos, etc.) please remember that the printed plate will be 4 × 6 inches; be sure that your illustrations are proportioned to reduce correctly, and indicate by blue pencil the intended limits of the figures. (Some "turn-page" figures with brief legends will be 3 1/2 × 6 in.) Magnification/reduction values given in text or figure legends should be calculated to reflect the actual printed size. An Abstract and a list of Key Words should be supplied at the beginning of each paper submitted, except for a very short article or note.

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Rhodora

JOURNAL OF THE NEW ENGLAND BOTANICAL CLUB

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RHODORA.—Published four times a year, in January, April, July, and October. A quarterly journal of botany, devoted primarily to the flora of North America. Price $20.00 per year, net, postpaid, in funds payable at par in the United States currency at Boston. Some back volumes and single copies are available. Information and prices will be furnished upon request. Subscriptions and orders for back issues (making all remittances payable to RHODORA) should be sent to RHODORA, 22 Divinity Avenue, Cambridge, Mass. 02138. In order to receive the next number of RHODORA, changes of address must be received prior to the first day of January, April, July or October.

Scientific papers and notes relating to the plants of North America and floristically related areas, and articles concerned with systematic botany and cytotaxonomy in their broader implications will be considered. Brevity is urged; please conform to the style of recent issues of the journal. See "Instructions to Contributors to RHODORA" at the end of each issue. Extracted reprints, if ordered in advance, will be furnished at cost. RHODORA assesses modest page charges.

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Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

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Cover Illustration

An original drawing, seemingly the only one surviving and perhaps the only one ever done for publication by Merritt Lyndon Fernald, used in part to illustrate his article on cranberry species which appeared in RHODORA No. 48 (Fernald, M. L. 1902. The variations and distribution of American cranberries. Rhodora 4: 231–237 & Plate 40). The drawing was rescued from a wastebasket by Dr. Bernice Schubert; it now hangs in the office of Dr. Carroll E. Wood at A. The original Plate 40 caption reads as follows: Fig. 1, *Vaccinium Vitis-Idaea;* fig. 2, *V. Vitis-Idaea,* var. *minor;* fig. 3, *V. Oxycoccus;* fig. 4, *V. Oxycoccus* var. *intermedium;* fig. 5, *V. macrocarpon.*

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THE NEW ENGLAND BOTANICAL CLUB 800TH MEETING

The Eight Hundredth meeting of the New England Botanical Club was held on May 4, 1984 following a dinner at the Harvard Faculty Club in Cambridge, Mass. This occasion was celebrated with a special program entitled "A Tribute to Merritt Lyndon Fernald" in which comments on Professor Fernald's botanical accomplishments, teaching, humor and philosophy were made for the benefit of the Club's membership by those of his students and colleagues who knew him and were in attendance. Additional comments were received in letters from many others.

The remarks delivered and selected sections of letters received are here published so that all readers of *Rhodora* may share some of the unique botanical history in which Prof. Fernald was so prominent.

MARY WALKER: I would like to open the 800th meeting of the New England Botanical Club. This is the 573rd meeting and also the 800th meeting; Dr. Howard will explain that anomaly later. In view of the nature of this meeing, we have decided to dispense with most of the formalities. I hope people have been signing the guest book; please continue to sign it during the evening. Instead of introducing guests, I would like to introduce all the past presidents of NEBC who are here tonight. We are honored to have nine of them. I will ask them all to stand as their names are called, and you can save your applause until they are all standing: Peter Ashton (I'm going backwards), Lynn Bogle, Alice Tryon, Gordon DeWolf, Bill Countryman, Richard Schultes, Reed Rollins, Dick Howard, and Ralph Wetmore. I hope that I haven't missed any past presidents. Thank you. Welcome!

Before I turn the floor over to our program chairman, Garrett Crow, I should say that this meeting, of course, is in honor of Merritt Lyndon Fernald. (I'm sure there are as many pronunciations of Fernald as there are of Thoreau. I come from Concord so if I'm not pronouncing it correctly, I will learn.) Since my student days, I've been familiar with *Gray's Manual,* starting out with the 7th edition; when the 8th edition came out, I realized what a monumental job it must have been for someone to produce that new work, much enlarged from the 7th edition. While putting together the poster exhibit for tonight, I came across a paper by Fernald written in 1939 entitled, "How Soon Will the Manual be Done?" (laughter) and asking botanists for time and patience.

While studying White Mountain botany as an Appalachian Mountain Club Hut Naturalist, I found Fernald's paper on soil preferences of certain alpine and sub-alpine plants, written in 1907, still to be a very useful document. In browsing through early and middle volumes of *Rhodora,* I've always been impressed with the number of articles by Fernald that were written during those years—from Volume 1 to Volume 53—not only by the number of articles, but more importantly, by the easy and fluent style in which they were written. Wherever he could, he injected human interest. That quality is badly lacking, I think, in botanical literature these days. When I offered to do the exhibit for this program, it was with a double purpose: partly to contribute just a little to the mighty efforts of Dr. Garrett Crow and Dr. Richard Howard in putting the program together, and partly to learn more about this unique man. In the course of the evening, I hope to learn still more. I leave you with one "wonder": I wonder who, among the younger people amongst us, will perhaps be honored by a meeting such as this; who will be revising *Gray's Manual*; who will perhaps be honored at the 900th or the 1000th meeting of the Club?

I'd like to turn the floor over now to our Program Chairman, Dr. Garrett Crow.

GARRETT CROW: Thank you. We're delighted for the wonderful turn-out here. It's been an exciting meeting for me, so far, to get to talk to so many people, and I hope it has been the same for you. I'd like to comment about the menu. Dr. David Barrington designed it; unfortunately, he was not able to come tonight. He's grading exams, which is a terrible excuse to stay away. I don't think I'd let that happen to me! He must be dedicated, in some way, to that group. But we have him to thank for the menu that's been prepared.

I do want to mention that the June meeting will be at the Arnold Arboretum and will begin with a tour of the arboretum in the afternoon. Watch for the mailing on that as to the details and then the evening program will be a talk by Peter Ashton on the Arboretum. But we don't want to take up any more time for such things. . . and I want to introduce Dr. Richard Howard who will be our moderator on this program, "A Tribute to Merritt Lyndon Fernald."

RICHARD A. HOWARD: Thank you very much, Garrett, Madame President. First of all, let me say that the 473rd meeting of the New England Botanical Club, which was the 700th meeting since its founding, was held in this very room. The head table was down at that end; I was the speaker, and I was asked to talk about the history of the Club. This speech was eventually published in *Rhodora,* and I still have a few reprints if any of you haven't read it (laughter); that was in 1973. This is the 573rd meeting, as our President said, being the 800th since the original establishment of the Club. The explanation for this binomial system is the fact that after 227 meetings, in 1921, the Club found that it was going to be subject to taxation by the Commonwealth of Massachusetts unless it incorporated. Hence, we started the numbering system all over again. At this rate, the 900th meeting will be held in June, 1995; I would like the program chairman to take special note of the fact that I shall probably not be available as a speaker (laughter). The chances are that my tombstone will contain that well-known epitaph that I've "gone to another meeting" (laughter). Ten or eleven years ago, at the 700th meeting, the senior members present were Ralph Bean, who joined the Club in 1909; George Safford Torrey from the University of Connecticut, who joined in 1912; and Donald White, 1913. All three are gone. Henry Svenson was the member who joined in 1919. He cannot be with us tonight but he sends his regards. Cap Weston, 1921; Ralph Wetmore, 1927, was at the head table; Cap is gone, Ralph is here. Hugh Raup, 1929, was at the head table; he cannot join us. Well, tonight our senior member is Harold St. John from Hawaii, who joined the Club on December 1, 1911. This was at the same meeting at which Fernald was elected President of the Club.

Now I'd like to set up some categories because I think Harold is the only member of the 70-year club of membership in the New

England Botanical Club. You'll hear from him in a few minutes. Those who have been members for over 60 years, who have been invited to attend and could not, but who sent their greetings, are Frank Seymour who joined on December 4, 1914, the last meeting in which Fernald was President of the Club; Henry Svenson, 1919; James Poole, 1920; and Lyman Smith, in 1923.

Then we can set up a 50-year category—those who have belonged to the Club for 50 years or more: G. Ledyard Stebbins, who we thought was going to come, joined in 1926, as did George Church, in 1926; Ralph Wetmore in 1927; Hugh Raup in 1929; Ernst Abbe and Dick Goodwin, 1930; Abbe is not here, Dick is. And while Gene Ogden, who is here, joined the Club in 1934, we're not considering him a member of the 50-year club, because he did not get elected until November of 1934! (laughter).

The history of the Club is very close to us. In December of 1895, William Farlow and B. L. Robinson assembled a group of friends in Farlow's house and proposed the establishment of a botanical club. Farlow's house was right next door—the location of the Carpenter Center, the Le Corbusier building that is right next to the Faculty Club. After two meetings, they decided they would indeed have a club, and the New England Botanical Club was officially christened on February 5, 1896. They gathered at various people's houses for dinner, and they had to eat, so there were four meetings in March, 1896. At the fourth meeting Fernald became a member, and it may be said that he dominated the club in his activities from that time until his death. You'll hear more about this as we go along.

I suggested for this program that we talk about Fernald, for those of us who knew him personally are certainly becoming fewer. For those of you who know him only as a name, perhaps some of the things we say will tell you about this remarkable man and his personality. He certainly was the right man in the right place at the right time. In preparing for this, we wrote to all of the old-timers and asked that they either tape something of their recollections of Fernald or write something out, give us a collection of stories or episodes, and we invited them to be present tonight. About nine-tenths of those we have contacted replied. Some of the stories were very short; some of them are quite good stories. And of those who are here, I'll ask about eight to talk for five or ten minutes. Then we'll open the meeting to others to fill in the gaps or add to the reminiscences. Of these manuscripts that I have on hand, some of them are rather significant. Hugh Raup has written a very nice essay; I would like to see it published. Lyman Smith has added some notes. Ernst Abbe defends the fact that he was the one who forced Fernald to reconsider the Nunatak Hypothesis on the basis of his work in Labrador. And Lily Perry, who knew B. L. Robinson and saw the transition to Fernald's administration, has given us some notes. I would like to suggest that, along with the comments of this evening, they be edited and considered for publication in *Rhodora.* We'll leave that to someone else.

Well, let me set the stage for Fernald. Merritt Lyndon Fernald was born in Orono, Maine, on the 5th of October in 1873. He was the third child of M. C. Fernald, who at that time was professor of mathematics and later became the first and the third president of the Maine State College of Agriculture and Mechanical Arts, now the University of Maine. At the same time, in 1873, Asa Gray was 63 years old, tired and overworked, as he said himself, in charge of an herbarium, a botanical garden, a teaching program, and several major projects on which he had to write. He had been president of the American Academy of Arts and Sciences for ten years. He had a worldwide reputation and the correspondence that went with it, and he was involved in fund-raising! Even in those days, Harvard had the edict, "Every tub on its own bottom" (laughter). The working budget for the Gray Herbarium in 1873 was $800.

Charles Sprague Sargent had just been appointed Director of the new Arnold Arboretum and had the additional duties of Professor of Horticulture at the Bussey Institution in Jamaica Plain. He also was the Director of Harvard's botanical garden, Gray's garden in Cambridge, and in this he relieved Gray of part of his duties. Now this was possible because Sargent had arranged it. He obtained from his father, Ignatius Sargent, and from H. H. Hunnewell, a promise of annual gifts of $500 each to provide Gray with a "pension" of $1,000 a year, which was more than Gray's salary, provided he resign and devote himself to the Flora of North America. Gray had, that year, made his last appointment of Sereno Watson as an assistant in the Herbarium. The next year Sargent appointed Watson as Curator in charge of the Herbarium. Gray accepted all this, Sargent in charge of the garden and Watson in charge of the herbarium, but he found himself on the outside, fighting Sargent's "audacious scheme" to move all botanical activities to Jamaica Plain. Gray died in 1888, the first year that a teenager, M. L. Fernald from Orono, Maine, sent specimens to the Gray Herbarium for identification. In 1889, Watson, who was then Curator, along with Coulter, issued the sixth edition of *Gray's Manual,* which was significant work because it expanded the range, the coverage, to the 100th meridian. In 1890, Fernald wrote to Watson:

> Orono, Maine, January 30, 1890, Dr. Watson: Dear Sir, I have just been looking at *Juncus,* #16, which I sent to you in the fall and am more convinced that it is not described in the Manual. [This is the Manual that Watson had just finished!] I sent you a specimen with more mature fruit than any I sent before. It seems to be something like *Juncus tenuis,* var. *secundus,* but the flowers are not restricted to one side of the panicle.

Watson wrote back to Fernald (and listen to this, if you think college recruiting is something new):

> I have been much pleased with the intelligent interest you have shown in the plants of your region. I have no idea what your plans or expectations for the future may be, nor even of your age or how far advanced you may be in your education; but, as a venture, I would like to say that if a career as a botanist has attractions for you (laughter), there is an opportunity open here for a young man who is willing to begin at the bottom and work his way upward (laughter). I am desirous of securing the services of some intelligent, capable, quick-witted young fellow to do work in the Herbarium that must be done. The work requires and *gives* familiarity with the Herbarium and the floras of the world in the way of caring for and distributing into herbaria the various collections that come in from many quarters. Opportunity will be given for study and advancement and compensation sufficient at least for support. If such a position has any attractions to you, I should be glad to hear from you.

Fernald wrote back immediately:

> The position you speak of does have attractions for me. I think that one thing I was made for was a botanist, as from early childhood my inclinations have been in that line. [The punchline comes.] I dare not say whether I would like the

> position or not. *We* are giving it careful consideration, and my father will doubtless write to you in a few days concerning it. I am the third child of Dr. M. C. Fernald, aged 17, and am in the freshman class at State College, located here, of which my father is the president. I know very little about "textbook botany," my work having been mostly in the field, and should I go to Cambridge, I should want to study as much as possible and do the required work satisfactorily. Respectfully yours, Merritt L. Fernald.

Well, Papa Fernald came down to see Watson and they talked about classical education for young Merritt. It turned out that Watson was able to arrange for Fernald to work half-time in the herbarium and, as a special student, take two courses at Harvard. Fernald arrived in the end of July of 1891, entered the Lawrence Scientific School and began an association that ended with his death in 1950, nearly 60 years later.

In this transition period, Fernald was publishing, believe it or not. He published notes on two carices of Maine in 1890. He published a list of special plants collected in the vicinity of Portland in 1891 that went through two new editions later on.

Fernald came here in the summer of 1891, and Watson died in 1892. B. L. Robinson, who had been Watson's assistant, was appointed curator in 1892 to follow Watson. So here we have Robinson, aged 26, with his assistant, this new student Fernald, aged 18, to work under him. The institutional projects of the Gray Herbarium at this period were supposedly four: revision of *Gray's Manual,* which was then the work of Robinson and Fernald, Robinson having the experience, Fernald having the experience in Maine; the continuation of the synoptical flora of North America which Gray had started, which was Robinson's responsibility; work on the vegetation of Mexico and Central America, in particular identifying plants from that area, the responsibility of Robinson, Greenman and Fernald. The collections were those of Millspaugh and Garner, C. C. Deam, Peck, Donnell-Smith, Rose and Lumholtz. The fourth project of the Gray Herbarium in those days was the indexing of newly described systematic entities for the western hemisphere. This is what we know today as the Gray Index. It was started down in Washington by Miss Day, who brought it up here to Harvard when Washington could no longer finance it; it has been one of the classic projects of the Gray Herbarium ever since.

Let me go chronologically here for just a bit and give you some of the highlights of this career of Fernald. In 1894, Fernald was the junior author of a paper with Robinson on the identification of the Hartman and Lloyd collections from Mexico. Robinson submitted this paper to the American Academy and it was reprinted, as was the tradition in those days, in the *Contributions of the Gray Herbarium.* In 1896, the New England Botanical Club was formed. Fernald joined at the fourth meeting. In 1897, Fernald published his own paper on the plants of Mexico, including a revision of the species of *Pectis,* and another paper which dealt with new additions to the flora of Mexico. Later in 1897, Fernald got his degree, a B.S. from the Lawrence Scientific School at Harvard, *magna cum laude.* In 1899, Volume 1, No. 1, of *Rhodora* was published. Robinson was the editor, Fernald was one of the assistant editors. The first volume started off with an editorial announcement. The first paper was by M. L. Fernald on the rattlesnake plantains of New England.

In 1901, Fernald started a project called *Plantae Exsiccatae Grayanae.* Now for those of you who haven't seen these classic labels, this was a scheme in which the botanist collected 125 specimens, or at least 125 sheets, and a special label was prepared in which the bibliographic details were complete. The plant was identified, all of the literature pertinent to it was cited, and down at the bottom it was noted where it was collected, and so on. These 125 were made up into centuries, and the centuries were distributed. The extra 25 over the 100 sets were to take care of those who had collected the centuries and wanted sets for themselves; so 100 sets were distributed. Over a period of time, 1500 sets were sent out between 1901 when Fernald started it and 1952, which I think is the last one, so for 50 years this project continued. Alone, or with Robinson, Fernald collected the first 54 sets, and you may be interested to know that the first numbered set was *Veronica serpyllifolia* var. *borealis.* It was collected in Fort Fairfield, Maine, on June 6, 1901. Now, if any of you know where Fort Fairfield, Maine, is located, you're better than I am because I had to go look it up. It's on the New Brunswick border in the very northeast corner of Maine; in those days, it was the end of the railroad. Fernald was exploring in 1901.

The second one that was collected has a very familiar name. It was collected in Van Buren, Maine, on August 13, 1901. It was a species published by Sereno Watson and was called *Pedicularis furbisheae* (laughter). And if you wonder why the plant became an endangered species, perhaps it was that Fernald, by himself, went up to Van Buren, Maine, in the type locality and made up 125 sheets of the thing and it hasn't been seen there since! (laughter).

In 1902, Fernald was appointed an instructor in Harvard College and he started to teach. In 1905 he was promoted to an assistant professor. In 1907 he was married; eventually they had two childern. In 1908, he collaborated with B. L. Robinson in the production of the 7th edition of *Gray's Manual.* Now the 7th edition of *Gray's Manual* is probably the poorest of the whole batch. It was regarded as a patch-up job. In fact, in a discussion later on, Henry Bartlett said that this was simply a cut-and-paste job, and few annotations were made on it. Fernald was not very proud of the whole thing, but it was Robinson's work Robinson and Fernald. Fernald, in several letters, says that he is going to start to work immediately and do a good job on the 8th edition.

In 1911, Fernald was elected president of the New England Botanical Club, as you see on your list here tonight. He continued in that capacity until 1915, when he was appointed Fisher Professor of Natural History. Robinson finally resigned in 1935 and Fernald was appointed Curator of the Gray Herbarium, serving two years; in 1937, he became the first Director of the Gray Herbarium, a title which he retained until 1947, when he retired. In 1950, *Gray's Manual* was published. Fernald died that same year on September 22, 1950.

In the February, 1951 issue of *Rhodora,* there are tributes to Fernald. There's a biographical sketch by Arthur Stanley Pease. There are sections entitled "Fernald as a Teacher" by Jack Fogg, who has since died; "Fernald as the Reviser of *Gray's Manual,*" by Henry Bartlett, who talks about the problems of the 7th edition; "Fernald as a Botanist," by Reed Rollins; and "Fernald in the Field," by Ludlow Griscom, who was a zoologist.

I knew Fernald in various ways from the time I came to Harvard in 1938 until his death in 1950. I was a student of Ivan Johnston, had been working with I. W. Bailey in the Biological Laboratories, and wanted to do some taxonomic work associated with the anatomy I had been doing, which meant using the Gray Herbarium. *Only* Fernald's or Weatherby's students used the Gray Herbarium as office space, so I created one of the first political crises of my stay around here by saying, with the support of the administration, that I needed table space in the Gray Herbarium. I was assigned table space in what was known as the Radcliffe Laboratory. For those of you who don't remember it, there was segregation in those days. At the foot of the stairs, going into the wing where the laboratories were, there was a little lab off to the left with a door on it that was usually closed. This was the Radcliffe Lab, and I was given space in there. At the end, looking out over the garden, was the space where the Harvard men had their quarters. This was meant to shame me, but my companions in those days were Bernice Schubert, Shirley Gale and Shiu-Ying Hu, and it wasn't so bad at all; Fernald did come in for lunch and eventually I got to know a little bit about him.

You look back on it and you say, "Fernald as a teacher." In these contributions that we have had sent in to us, the name "Botany 7, The Flora of New England and the Maritime Provinces of Canada," is mentioned often. Botany 10 was "The Classification and Distribution of Flowering Plants: Advanced Studies on Special Topics," and here Fernald roamed. He could do anything he wanted. Then there was a course—and I haven't been able to find the name or the number of that which we called "the drawing course." This was divided into two semesters: one on the monocots, one on the dicots. Fred Taylor brought his bound drawings, and they were on display earlier tonight. The work of that course and all it was, was that Fernald pulled out specimens of various groups and put them down and said, "Draw them." It is also said that from these art works Fernald selected the artists for his later contributions and publications.

"Fernald as a collector?"—I apologize; I was not able to find his field books to find out what his total numbers were. They are significant. He spent his summers collecting; I am sure you will hear about the field trips he took with students to Cape Cod and elsewhere. He roamed from Nova Scotia and the Gaspé to Virginia. Frank Seymour wrote to me that the students used to call certain lectures, when Fernald started talking, as the "gas-bay" lectures, as Fernald was so windy about it. He started *Plantae Exsiccatae Grayanae,* as I've indicated; there were 1500 numbers of that. The majority of them were collected by Fernald; 1457 was the number of *Proserpinaca palustris,* the last one that he collected. Of the last centuries, incidentally, ten were collected by R. A. Howard and students in Cuba. And while it seemed a little strange to be adding Cuban plants to this, we found that one of the most popular ones that we sent out was *Rhizophora mangle*. It had the greatest fan mail because this common mangrove was not well represented in herbaria, and we had included the specimens of flowers and fruit and photographs. In the photographs, I followed the lead of Walter Hodge who had been collecting in Dominica *exsiccatae* sets for the Gray Herbarium, and his photography was better than mine. You'll still see some of these *Charianthus* and Melastomes under the *Plantae Grayanae*. Regrettably, it stopped; it was a good series.

"Fernald as a scholar"—It is said that he published 750 papers; I don't think I've read them all. *Gray's Manual*—a monument to anyone—is the last of the big manuals written by one individual. His work on the persistence of plants in unglaciated areas is outstanding—the Nunatak Hypothesis that Abbe challenged. The monograph of the linear-leaved species of *Potamogeton* is still cited as the outstanding model monograph of all time. The plants of the "wineland," with its discussion as to where the Vikings landed, is here. The edible plants of eastern North America is another; whether it was Kinsey's manuscript or Fernald's is still a point of debate.

"Fernald as an editor."—Well, he was in Volume 1, No. 1, of *Rhodora*. In 1929, in Volume 31, he became the editor and continued until his death. The October issue of 1950 is the last to bear his name. The November (1950) issue has the last paper authored by Fernald in *Rhodora*. Its title is, "Why So Many Careless Books on Trees and Shrubs and Other Plants?" (laughter). This was characteristic of Fernald's reviews or his criticisms; he didn't have a blunt pen, I'll tell you that.

The last paper bearing Fernald's name was in the January issue of 1951 in *Rhodora* and is "Botanizing on the Gaspé Peninsula, 1902–1904." There is an editorial note that "until the day of his death, Professor Fernald had been working on a journal account of the field trips to the Gaspé, project to cover the years 1902–1934." He had sufficiently completed the years '02 to '04 to make this portion of the manuscript publishable. We wish we could have had the rest of it, because it's good.

He edited the *Contributions of the Gray Herbarium*, and while these were reprints of papers published elsewhere, with early ones from the *Memoirs of the American Academy* and the later ones from *Rhodora*, they were significant in the distribution of publications that led to exchanges with the Gray Herbarium. An early editorial note by Miss Day warns that these papers are to be cited on their original dates and pagination and not by what is in the *Contributions*. The first original article was *Contributions* No. CLXV, which was a miscellany in honor of Merritt Lyndon Fernald at the time of his retirement. Fernald's last contribution to the *Contributions* was in 1949, but I think Carroll Wood has the honor of being the last author reprinted in *Contributions* for his work on *Tephrosia*, which was in *Rhodora*.

"Fernald and the New England Botanical Club"—Well, he was president, he was Curator of the Herbarium, he was on the council, he was the Editor. I think my fondest recollections are of the continuous competition he had with E. D. Merrill. Merrill came to Harvard as the Coordinator of Botanical Collections—Supervisor of Botanical Collections and, in theory, was Fernald's boss. They were both short people. They were both very important people, and they knew it. And they were both from Maine and that's equally important! It is very clear in my recollections that Fernald never stood up to say anything but what Merrill popped up afterwards to say something. And if Merrill started first, Fernald stood up and said his piece, too. One of the minutes in 1911 probably summarizes it very nicely: "Mr. Fernald filled in the remainder of the time by giving a very interesting account of his excursion on October 12 to Wallum Pond on the Rhode Island line in search of *Sclerolepis*. He secured fine flowering specimens in both Rhode Island and in Massachusetts, thus adding this new plant to our state flora." If you read through that, the plant was known from Rhode Island, but he found a pond that was on the line; when he got around the pond, it was in Massachusetts, so it was an addition to the state flora.

Well, I have kidded a bit here about Fernald, and yet I have deep regard for what he has done, and I know the others have, too. I would like to ask other people to come up here and talk for five or ten minutes. I pointed out to you that Harold St. John was elected at the December 1 meeting in 1911, when the annual meetings were held at 3 Joy Street, which I think is where the private environmental organizations rent their offices from the Appalachian Mountain Club next door. Meetings have been held at various places; in fact, my first recollection of the Club was on Newbury Street when we met in the quarters of the American Academy. President Deane was in the Chair, and Merritt Lyndon Fernald was elected President for the next year at this meeting at which Harold became a member. There were 33 members present; the speaker was Mr. Deane. His title was "The Mystery of the Maple Sap Flow," and he concluded that nothing positive is known as to why sap rises. Emile Williams was the Recording Secretary, and there was a Treasurer's Report. I thought you might be interested that the Balance on hand at this meeting on December 1, 1911; it was $151.51. The income during the year was $722.98; incidentally, the expenses were $799.83, which meant that at the end of the year the Club had a balance of $74.60. As to the income in that year, $645 was from dues. Now keep in mind that these were dinner meetings, so everybody ate. Later on, we went down to ice cream and donuts and ginger ale, and now we're down to cheese and beer and so on. Things have gone downhill badly in the years, but costs have gone up, too. Dues produced income of $645, and there was an entrance fee, which that year was 60¢. The interest on the bank deposit was $17.53, and Mr. Treasurer, please note: Income from the sale of empty beer bottles was 45¢!

Now I would like to ask Dr. Harold St. John, our senior member, to give us a few comments. Harold.

HAROLD ST. JOHN: Thank you, Dick. I'm very glad to be present here because the New England Botanical Club played a very important part in my development as a botanist. At meetings of the Club, I met numerous, dedicated, interesting, fine botanists, so I'm very glad to be present at this meeting. Now, I can't help being here because I was born a botanist. I was collecting plants—I was well along—at the age of six, and I've collected plants ever since.

My schooling was in the public schools of Brookline, Massachusetts, mostly, and my schooling was entirely in the classical trend, in the classical program. I never had a course in botany until I came to Harvard College. The first course I had to take was Botany 1, the elementary course, and it was the most boring, stupid course I ever had (laughter). It was taught by a physiologist (laughter), and he spent most of his time in the lectures trying to imitate life; and as far as I'm concerned, he never did! (laughter). The next year I was able to take Fernald's course on systematic botany, and what a revelation that was.

Fernald also was a born botanist. He loved his subject; he had broad knowledge of it. He wrote beautiful English, he spoke eloquently, and his enthusiasm for his subject just bubbled out of him. You couldn't help feeling the enthusiasm which he had for his subject.

I became his teaching assistant, I think the next year. If not, the second year after that. I handled the lab sections of his courses in Harvard and in Radcliffe, carefully separated. After Fernald lectured to Harvard, the next hour, normally, he gave the same lecture to Radcliffe in the next room. "Why can't I talk to the two of them? Why can't I have a single audience?" That was one complaint that never ceased.

I think it was in my junior year that Fernald invited me to be his field assistant on a trip to eastern Canada. On that same trip, he had as one companion E. B. Bartram of Philadelphia, who at that time was studying the flowering plants. Bartram was a big, rangy, husky, outgoing friendly sort of a person. Not long before, he had come back from the Spanish War, and he thought there was no use in going to college. He was already a man, his own. Well, he got into work in Philadelphia in the Moore-Field Company, which made steel wire. And he proceeded to move up in the ranks into administration. Apparently he was very well remunerated and, by the time he got to be forty, every time you'd meet him he'd say, "Well, I'm going to retire; I'm going into botany; I've made all the money I could ever use; I'm going to retire." But he took another ten years for it to happen. The other companion was Bayard Long, also of Philadelphia, who was a very keen, lean, nervous, rather irritable, easily offended person. So we had a mixture of personalities there. But Fernald, in the field, was a different person from his characteristics that he showed in the laboratory. He was friendly and jolly and cheerful, and no longer was he criticizing your English or pointing out what you concluded in a paper you handed to him, that you hadn't proved what you concluded. In the field, he was jolly and nice and friendly; he seemed like a different man. We spent the summer on Prince Edward Island and in Nova Scotia. And the next summer, the same quartet worked on the Magdalen Islands in the Gulf of St. Lawrence and in western Newfoundland. Then the next summer, Fernald raised the money, I think all of my expenses for one summer was a hundred dollars. He sent me out to Sable Island, off the coast of Nova Scotia, 200 miles out to sea, east of Halifax, a 20-mile sand-dune island, which is along the stretch of sandy coastal country that runs from Virginia, southern New Jersey, Long Island, Cape Cod, and out to sea finally to Newfoundland, the Avalon Peninsula. That was a very interesting expedition. Two years after that, I went with Dr. C. W. Townsend and cruised in a 40-foot schooner, without auxiliary, 600 miles along the coast of southern Labrador. Those opportunities were made possible to me by Fernald.

I am wandering along from one subject to another, not knowing how to prepare a talk like this because I figured I was following Dick Howard and he would hit all the high spots, and I'd try to fill in a few of the low spots.

Every five or seven years, I used to come back to the Gray Herbarium from my positions in the west or in the Pacific Ocean, and always I enjoyed seeing Fernald. I remember, toward the end there was a second-story balcony inside of the Gray Herbarium in the room with most of the cases. At that time he had eyeglasses, oh, 8 or 10 mm thick. He couldn't see you across the room, but one day he was up on that balcony and looked down—"St. John, you're gettin' bald!" (laughter). He also could see things closer to; that is, he had these glasses on and a lens and the sheet with the plant specimen was, at most, 10 cm from his eye. Nobody else could see any difference, but he could see a new species at that distance (laughter).

Well, I thank you for you attention. (Applause).

R. A. HOWARD: May we all be as vigorous when we've been in the Club for 70 years, too (applause). James Poole, who joined the Club in 1920, felt that he might be able to make the trip down from Hanover, but finally it was decided that he should not make the trip. However, we have an interesting situation here because although he was one of Fernald's students, so also was was his daughter. So we have two generations represented in Margery Poole Taylor, who is representing not only herself but her father, Jim Poole, of the NEBC class of 1920. Marge.

MARGERY POOLE TAYLOR: Jim Poole is sitting in Hanover tonight, at 95, frustrated utterly that he isn't here, I'll tell you that!

He would just love to be with you, and he has given me a paper to read to you, but he'd much rather do it himself. He writes:

> I'm most grateful for the invitation to attend this 800th meeting of the New England Botanical Club. I am particularly happy to have the opportunity to honor Professor Fernald. I had the privilege of attending his course in Taxonomic Botany in 1915–16. In my estimation, it was outstanding among all my graduate courses. His lectures were interesting, and occasionally delivered by bits of MFL wit or humor. His field trips, several of them, to the lake shores of Cape Cod were unforgettable experiences for those in his class. I recall one instance illustrating his keen faculty for recognition of differences in characters of taxonomic importance. At that time, my father owned an Oldsmobile touring car, equipped with jumper seats in the tonneau. I borrowed it for one weekend. Its capacity made it possible to take Professor Fernald and the class for a trip to the Housatonic Valley with occasional visits to areas of botanic interest along the way. As I recall the event that I am referring to, we were bowling along at 35 miles an hour when Fernald, in the front seat, said, "Whoa, whoa!" I stopped as quickly as the brakes permitted, Fernald jumped out and ran back a few yards to a grassy area beside the highway. He soon returned with a specimen he had spotted as a different variety of Bluegrass, probably a variety of *Poa pratensis,* and this he had recognized from a car, at that high velocity! (laughter). We were in the town of Charlemont on old Highway 2, between Greenfield and North Adams, in either April or May of 1916. It would be interesting to discover that particular specimen in the Gray Herbarium (and Carroll Wood is going to look into it). I am very sorry and disappointed that I am not with you and have to remain in Hanover. Hearty greetings to any of my old friends who may still remember me.

Dad is 95 this weekend and I do have a birthday card for those of you who knew him; please come up and sign it, if I haven't caught up with you yet.

Now, about myself. I took his course, I think it was in '36. When I got to Harvard, I discovered I had some "uncles." One of them was Ralph Wetmore. He had been a grad student with my Dad. And Fernald was another one. And they were a little bit amused, I think, at this young "chick" coming in there trying to be a botanist. But I think from the age of three, as Harold St. John said, I was imprinted as a botanist. I just was one from the beginning. I have continued in my field in many directions, but my days at Harvard with Fernald were among the things I remembered particularly. I have some pictures taken on a field trip of that time; and if any of you were on field trips in '35–'36, I can't identify anybody but Fernald and myself, maybe you are in it —who knows? So come up and tell me. I did include a magnifying glass for those of us who need it. Do come up and talk to me if any of you know Dad. He is still at the Jesup Herbarium as a curator. He goes up three or four days a week and loves being up there. Thank you. (Applause).

R. A. HOWARD: Marge, the current Index Herbariorum lists James Poole as the curator of the Jesup Herbarium in Hanover, as you just mentioned: 95 years old, the only staff member ever listed for the herbarium. Please give him our regards and best wishes on his birthday. Sorry he couldn't be here.

I chose for the next speaker a man who came to Harvard in '26 and joined the Club in '27, and who today is one of the best-loved of the senior staff members. Those of us who are much younger shared his courses and his care and concern for students and have a very high regard for Dr. Ralph Wetmore. Ralph.

RALPH WETMORE: Thank you. It's certainly a privilege to be here. There have been times when I thought I wouldn't be, but I'm very glad that I made it! Honest. I have been here since 1921 when I came after my undergraduate training, for my graduate work; I happened to have chosen Fernald's course the first year I was here. I was down in the Museum; that's where the Biological Laboratories were at that time; the Biology Building was not built until the early 30s. But I confess that, so far as maintaining the botany was concerned, Professor Fernald's course—I'm still a rooter for him. I'm very glad to speak here in his interest. I wish he could be here, too, to hear some of the things that have been said. None of it was said, that I know about, inimical in any way to his entire prestige, in either his lectures, which were continuous, because they followed the manuscript of the 7th edition of *Gray's Manual of Botany*. But as far as he was concerned, there was no question that he was loved by all his students. His field trips were phenomenal. This has all been said, but I can't help but repeat. After I came here on the staff in 1926, I must confess that for a period of years I went on every field trip I could get to. One incident that I do want to refer to just a few minutes, but particularly do I want to point out that from the time he started on the long corridor down to the extension of the Gray Herbarium used for his and others' lectures, I must confess that you knew it was Professor Fernald coming. Most people took one step at a time, but he "clicked" on the floor twice with each step, and I don't know how he did it; I never did find out (laughter). It was his walk—quite unusual—and it was always present.

His classes were taxonomy to be sure, and taxonomy of the regions that he had covered in his lifetime, and botanized, but they were different. There were so many incidents of his particular traits on a field trip that were amusing and interesting that he always used to spice his lectures, and believe me, they were spiced!

You've heard a number of things of his way of doing things, but I want to mention one incident that took place, and think part of his life would never have happened if it hadn't been for the football captain who was there that afternoon. He had been busy all the fall captaining the football team, and winning, and late in the fall and early the next spring, when there was no football, he used to go on field trips, and in one particular one, we had gone up to southern New Hampshire just at the time when the first touch of spring was present. You could see the beginnings of green and we hoped to find a few things in bloom and that we did. Professor Fernald kept close to the edge of the water of the stream that we happened to be on at that particular time. It was on the edge of a millpond, if that means anything to you, the backing up of the water in the spring of the year so that they could do whatever sawing they needed to do for the summer before the brook or river dried up. In this particular instance, he bent down close to the edge of the millpond which was quite a number of feet deep. I have no idea; I didn't test it, but in this particular case, he got too close to the edge and disappeared! (laughter).

We stood there—dumbfounded (laughter). Nobody did anything —not a thing. Unfortunately for the rest of us, and to our shame, we saw the football captain peeling off his clothes. He got the outer clothes off and in he went. In just a few minutes, he bobbed up to the top. It was clear that he was being held down by something; but we pulled him out to the shore and in his one hand he had hold of Fernald's hand. We got Fernald up on the shore and laid him out. To our surprise, he had the digger in his hand. One end is a spade-like thing that you can dig with, which he dug up roots of his plants and the other end was broad and he could get the top part of the plant out, with the entire root, whether it was an herb or had a root close enough to the surface. On this particular instance, when he got to the surface, when we fetched him out, he had the digger still in his hand. He probably would never have told the details of what happened at that particular episode; it was about mid-career, I suppose, about 1927-28—I don't remember the dates, unfortunately—but one will always think of him, those of us that were present. There may be one or two here who were there on that trip, I don't know, but I must confess, it was one of the outstanding achievements of the football captain (laughter), rather than any of the rest of us who were somewhat ashamed, I'll admit. I'm not going to say anything more about Professor Fernald. I'm on his side, rooting for him. If he were still here, I would tell him so. Thank you very much. (Applause).

R. A. HOWARD: Thank you very much, Ralph. The point of these two stories you've just heard is that Fernald did not drive a car and depended on others for transportation. Perhaps some more Fernaldian car stories will come out, but Ledyard Stebbins tells of one graduate student who had a car that Fernald dubbed "*Juncus canadensis.*" True to its name, the thing broke down and so Fernald re-christened it "*Juncus inutilis.*" Incidentally, the other part of Ralph's story is that Fernald couldn't swim, and yet he took groups of students out in the field. This was my experience with him: on going down to the Cape, we stopped at the first wet area that was seen, Fernald led the party, and we crossed the wet area. He generally knew when it wasn't over his head, so we didn't repeat that episode, but we got wet. For Fernald, it was up to his waist; for me, it was up to my knees (laughter), but nevertheless we got wet. When we got to the other side, he simply walked around the pond, we got back into the cars and drove to where we were supposed to go. This was Fernald's philosophy: if you get your students wet immediately, it doesn't matter what they do during the rest of the afternoon, and it operated very effectively.

When Fernald retired in 1947, Lincoln Constance was asked to come to Harvard and, as he says in part of his letter here, he was put in charge, but a few weeks later he was "appointed Acting Director since the Harvard bureaucracy would not honor my signature unless I held a formal title. My principal responsibilities were actually only two: to keep the Gray Herbarium running for the year, meanwhile to assist in the selection and confirmation of Fernald's replacement, and to convince Fernald that he *had indeed retired.*" He talks about Fernald's replacement in this way: "I first visited Cambridge in 1942 just after Reed Rollins had accepted an appointment to the faculty of Stanford University, and I asked Professor Fernald if he was not as greatly pleased as I was. Fernald looked at me quizzically for a moment and then snapped, 'They're pretty radical out there.' So much for Clausen, Keck and Hiesey and what Stafleu calls the 'birth of biosystematics'."

Fernald's successor has proven his merits; we've known him a long time now, and he is retired. He joined the Club in 1937, so we're getting closer in the generations here. Dr. Reed Rollins, incidentally, has made a tape which we can use as a manuscript later on and we'd like to have him say something now. Reed.

REED C. ROLLINS: Thank you, Dick. I'll be fairly brief because we're getting down now to the point where it's "modern history," at least not quite so ancient. I suppose if I wanted to, as an administrator following Fernald, I could spend a lot of time tearing him apart. But I'm not going to do that because, first of all, there's no point in it and secondly, I don't think he would deserve to be torn apart. There is so much on the positive side that this more than counterbalances the minor things that I ran into when I came to take over the Gray Herbarium as Director. Fernald was not an administrator and I think those of you who knew him would admit to that immediately. He was a botanist; in fact, he was a *botanist's* botanist. He lived and breathed botany and he wasn't really interested in anything but that, so he had difficulty dealing with the bureaucracy that then was minor compared to now in Harvard University (laughter). So I must say that even Lincoln Constance, in his one year of Herculean efforts to sort of make the way for me less difficult, couldn't manage to bring the Gray back into its best form by the time I arrived in 1948.

One of the tragedies that did occur, and which I always thought I might have done something about, was the demise of the Botanical Garden. I don't know how many of you remember or know that, but by the time I arrived on the scene here, the Botanical Garden had gone the way of all flesh. The best plants had been taken out and moved to the Arboretum to save them and the bulldozers were busy tearing up the Garden and eventually housing was put there.

The development then proceeded in a rather different way. The Gray Herbarium, as an isolated institution, became somewhat untenable and eventually was moved into its present location. Fernald wouldn't have liked this and, in fact, was very much opposed to the demise of the Garden even though he took very little interest in it. A rather amusing incident had to do with the naming of the streets that now go across the old Botanical Garden. Those of you who know Cambridge know that the street on the back-side of the old Gray Herbarium building is known as Robinson Avenue and the one on the front-side is known as Fernald Drive. When we broached the subject of naming these streets, Professor Bailey was then in charge of the general area—he and I consulted on it—and we hatched up the idea of naming them for Fernald and Robinson because Gray was already honored by street names. There is Gray Gardens East and Gray Gardens West and Gray Street, and it seemed appropriate to have more botanists commemorated in this way. We wanted to sound Fernald out a little bit before proceeding. Some of the people had said that he is rather a vain man and he really would like this sort of thing, but that his response would probably be negative. And indeed it was negative, on the surface, but after we probed a little we could see that he was pleased with the idea and so we went ahead. I'm sorry that we don't have projection facilities because I do have a slide here that shows Fernald in front of Fernald Drive and he was rather proud to pose for that picture.

Coming along late in the evening as I am on this program, I find that the stories that are told by the people who knew Fernald in his early days are rather of a different character than the stories that I recall. I think this is largely due to the fact that Fernald, as he progressed in his career, rather had a little different view of what he should be doing. He became completely engrossed in the revision of *Gray's Manual.* He did field work and he did write about it, and his written work had all of the characteristics that have been mentioned. He wrote very well. But he, somehow or other, around the Herbarium itself, seemed to concentrate more truly in his work on the Manual, so that he rather resented interferences. And the students, in particular, were not as freewheeling as far as going to him was concerned as they might have been, I think, at an earlier period. Although, in talking to Lyman Smith the day before yesterday in Washington about Fernald, Lyman Smith said, "You know, Henry Svenson, one of his early students, I felt very sorry for, because Svenson was scared stiff to go to Fernald and discuss his thesis in detail. He thought that the thing to do was to prepare the thesis completely and then go to Fernald, so he proceeded in that fashion. Eventually, he went to Fernald and Fernald found something wrong with the way Svenson had prepared the descriptions. Fernald made him make changes, so Svenson had to go through his entire thesis, altering I don't know how many species descriptions. The same corrections had to be made over and over again all the way through." Lyman thought it to be a great shame that a graduate student had to go through this kind of thing.

I won't say much more. I have quite a bit more written down here. I could talk about Fernald's closest friends, for example. I believe J. Franklin Collins from Providence, Rhode Island was one of his best friends. When Collins died, he left Fernald his set of large glass projection slides, a rather extensive collection of photographs taken during their field trips together over an extended period of time. Fernald used these considerably in class along with the slides he had made himself. He was particularly interested in the distribution of plants through the areas that have been mentioned, from the Pine Barrens of New Jersey all the way up the coast, particularly Long Island, Cape Cod, and then further north. He often spoke of the plants of the coastal strip.

Bayard Long was another of his very close friends. Fernald, as some of you certainly know, was a rather frugal man. He certainly was well-off when he died. He played the stock market and Bayard Long, who also played the stock market, was his confidant in this matter, Fernald would take his tips from Bayard Long. Fernald took this seriously to the point where when we would go on a field trip, he would say, "Now we must stop at a Texaco station because I've got stock in Texaco."

We had memorable trips to the Cape. Fernald would hire a cottage where the class would stay, and we would work out of there. I know that Walter Hodge, for example, took pictures of some of these trips and a few of these were included in a series of articles published in *Rhodora* at the time of Fernald's death. Students liked to play little tricks on Fernald. He was always very, very interested in what he was doing and would get so engrossed that he didn't really pay any attention to anybody who might be clowning around him. And so it was often the case that a student would pick a long spear of grass or maybe a dried-up *Solidago* infructescence with a piece of stem on it and then they'd stick this into his hat, you know, and it would be towering up above. I remember one picture, I think, Walter took with the hat so adorned. But, these kinds of things were fun for the students and he, I'm sure, would have entered into it more at an earlier period in his life but didn't do it so much at that particular time which was well toward the end of his teaching career. Thank you very much. (Applause).

R. A. HOWARD: Thank you, Reed. The Gray Herbarium in my period was largely a one-man show. As I indicated to you, Fernald was in charge certainly. But there was a second person around there—Charles A. Weatherby, who graduated with an A.B. from Harvard at the same time that Fernald got his B.S.; that was in 1897. Weatherby was a specialist in the pteridophytes and he was entitled to have students. That was why I was out of place as being Johnston's student. One of Weatherby's students—and perhaps looking in from the side—was Dr. Rolla Tryon. Rolla, will you take over for a few minutes? Maybe I should say "looking in from the top," because if any of you remember the atrium that was the Gray Herbarium, you went up the side steps until you got to the top balcony, then in the middle of the front of the building there was another set of steps that took you into this aerie that was Weatherby's hang-out.

ROLLA TRYON: Well, what I wanted to speak about takes a little different tack than some of the other people have, and that was to mention the contribution of Fernald to the subject of Plant Biogeography. His field work has been mentioned, and certainly Fernald was an avid collector and I suppose that, with the others he collected with, he must have taken at least 100,000 sheets, probably more (not that many of each kind because they often collected in duplicates). And it's been mentioned how he collected, for example, in Virginia, Massachusetts (particularly Cape Cod), Maine, Nova Scotia, the region of the Gaspé, upper Gulf of St. Lawrence, Newfoundland, and rather later, northern Michigan and adjacent Ontario. This collecting was clearly directed toward two lines of research: one, that of understanding the species of the *Gray's Manual* area better and getting their taxonomy straightened out, and the other was toward biogeography.

I think that Fernald's genius, in fact, was to synthesize this taxonomic research, the biogeographic research and his field work essentially into one whole. They were not at all separated. His biogeographic method, which he developed to a point which still serves as a model today, was first of all to see unusual ranges, particularly disjunct ranges, and to see that a considerable number of species had essentially the same kind of disjunct range. Then he would begin to look for paleoclimates, paleogeological explanations that might afford a clue to *when* and in what direction these ranges that were now so isolated were once, in fact, connected. And so he sought the explanation in recent geological history. If you read his writings on biogeography closely, you'll find that they're full of the ecology of the species he was dealing with, not just the distributions themselves. And particularly in relation to his Nunatak Theory, as well as others, he was in fact nibbling at the edges of population genetics. To those of us who knew Professor Fernald and heard what he had to talk about, it might be surprising that he would ever get into that kind of subject at all. Of course, he wasn't very deep into it, but he did have to deal with these very local endemics that did not spread in their distribution, and he was considering problems related to that.

His major theories I think many of you are quite well aware of. One of the first related to eastern North America and Europe. In many cases he was grumbling greatly because our species here were still under the name given in Europe. He did a great deal of work in sorting out these species and finding, in fact, that many of them were closely related but different species. In this respect, he proposed a theory of an earlier North Atlantic connection, when at least there was much less water there, and that many of these species could have migrated between North America and Europe. There also has been mentioned his work on Nunataks, which related to the Gaspé area particularly, and to the west, in which he envisioned these regions as having escaped the last glaciation and species were disjunct because they were able to persist in these very small areas. Mount Albert was one of the most famous of those. And then, also, there was the matter of the coastal plain. This involved Cape Cod, Nova Scotia, and Newfoundland. Almost all of the areas where he went to collect had biogeographic significance to him, which is why he went to these areas. These coastal plain elements are now very disjunct from Cape Cod to the north, and he envisioned a shelf off the present coastal plain that later had subsided. Originally, however, it could act as a migration route.

At the time Fernald was working, the geological evidence for much of this—the evidence that he required—was not, in fact, present. The geologists were rather slack in Fernald's opinion (laughter), and he didn't hesitate to say so in print. In fact, he rather goaded the geologists to do some more work and give him the kind of information he needed for his historical explanations. Whether in fact these theories and these explanations are eventually accepted or not as right or wrong is not really critical to Fernald's contribution in biogeography. He had two, certainly, lasting contributions. One was his very strong influence on other botanists; for example, Hultén, Porsild, Raup, Victorin, Fassett, Hodgdon, and the many colleagues and many students of these people as well. Also, he published a vast amount of accurate data on ecology and the geography of species and integrated this into a coherent whole which stands as a model without respect to the precise accuracy of his conclusions.

I think, finally, that it is fair to say that Fernald lived in the Golden Age of Plant Biogeography in America, and he was the central figure in it. (Applause).

R. A. HOWARD: Thank you very much, Rolla. I would like to submit a written contribution I received, a charming several pages from a foreign graduate student of Professor Fernald's last class in Harvard University. While it may be a little long to have all of it, is Shiu Ying here? Yes. Dr. Hu, would you please tell us a couple of those stories at least that I found so interesting?

SHIU YING HU: Thank you, Dr. Howard. In the summer of 1947, Professor Fernald completed his teaching career in Harvard University. I was fortunate enough to be a student in the last class he taught. However, he was not my first teacher because his course was in the spring. Before him, I had Professor Paul Mangelsdorf for

Economic Botany, Professor Karl Sax for Cytotaxonomy, Professor Elso Barghoorn for Paleobotany, and Professor Elmer D. Merrill, my major professor, for a 300 course. I found that Mangelsdorf's and Merrill's courses were manageable; Sax's and Barghoorn's courses were pretty hard. Both of those men spoke very low and I couldn't get the words—*they spoke half way* and swallowed the rest! (laughter). And Fernald's course was, to me, just incredible. The reason was that Fernald did not teach with botanical language, so I just couldn't catch what he taught. I was poorly prepared for his witty deliberation, clever statements and very amusing stories.

Professor Fernald's course was held in the old Gray Herbarium building situated in the corner of Garden Street, Linnaean Street and Robinson Street. When I went there, the first thing that attracted me was a beautiful rock garden just in front of the right wing of the building, and in the early spring, it was just beautiful. The class consisted of about eight students; most of them were American G.I.'s. There were two foreign students; John Constable from Great Britain was an undergraduate, a senior, and of course, myself. The subject matter of the course was botanical history and phytogeographical principles. Fernald didn't have an outline for his lectures because everything he had was in his head, and for his guide of the botanical history, he used a large file that Mrs. Asa Gray collected. Those big books—I actually measured for this talk—were 400 cm long, 275 cm wide, and 10 cm thick! There were many volumes.

At that time, we had classes in the Bio Lab and then we had to walk all the way across campus to the Gray Herbarium, which was opposite the Observatory. When we arrived, Fernald would wait for us with one big volume, usually open, and he started from A to Z. It was my first year in America. All the names sounded queer to me, and I just couldn't catch the sounds. Finally I moved my chair to his side, so that as soon as he opened that big book, I copied the names!

The laboratory work, as Dr. Howard said, was in the right-hand wing of the Gray Herbarium on the first floor. The large room was for Harvard men, and the small room, I was told, was the Radcliffe room. Dr. Howard was on one side and I was given a table, and Professor Fernald came to have lunch there by himself every day. The first time I saw Professor Fernald having lunch in the Radcliffe room, I made a terrible mistake by American standards. It was done partially because of the things he ate, and partially because of my ignorance of American academic life. Fernald came to the Radcliffe room, sat there, opened a small cake-box, took out a banana, and a sandwich, and then began to chew a big raw carrot without peeling or cutting it. I was horrified! (laughter). In order to explain this incident, I need to tell you something of my background. The rural people of the lower Yellow River region in China eat raw onions, garlic, green pepper, coriander, tender parts of Chinese cabbage and raw carrots. But the people in cities, and especially the literate people, don't eat these things. I learned this difference through a very bitter experience in a boarding school. I was sent to a boarding school at the age of 11. Approximately 90 percent of my classmates were 4 to 8 years older than I. One day a relative of mine brought a bundle of presents from the village, and in it there were some carrots. I was so happy for my gifts and began to eat my carrots. A big city girl ridiculed me, saying, "Look at this little barbarian girl from the country. She is eating a raw carrot." I quickly hid my carrot and from that time on I had never had a raw carrot until I became Americanized. So when I saw Professor Fernald chewing that raw carrot, my hidden wounds suddenly surfaced. I walked to Professor Fernald. I said, "Professor Fernald, do you eat raw carrots?" (laughter). As he chewed, he said, "Why not? Carrots are good for you." I said, "I heard people say only barbarians eat raw carrots." (laughter).

Well, you know that the Gray Herbarium was a small family, and news went out very fast, so before the end of that afternoon everybody knew something I did with Professor Fernald! There was a Miss Marjorie Stone who helped Professor Weatherby with the Gray Index. She was a very serious person and she came to find out if I really did say, "Professor Fernald, you are a barbarian!" (laughter). Well, don't laugh. The better part is coming. You see, at that time, it was only a few months earlier that I came from China, which was isolated for eight years and was bombed by the Japanese. During those years, unlimited inflation ruined the lives of college professors. Instead of taking home money as salaries, (money didn't mean anything), the professors would, for each person of the family, take home three bushels of rice. For example, a professor with a wife and two children would take home 12 bushels of rice for salary, for food and for exchange of other things. So during the war, the Chinese professors really had a very hard time. When I came, I saw Professor Fernald chewing a raw carrot and I thought that he was undergoing similar economic hardship (laughter). So as I walked out of Gray Herbarium that afternoon, I decided to do something for this "poor old man." The next time I came from class, I brought two large *Malus* Delicious apples. When I saw Professor Fernald starting his carrot, I held one apple in each hand behind me and approached him. I said, "Please do not eat that carrot (laughter); eat these apples." I put the apples in front of him, and he took up one and ate it. Later in that afternoon, I met Carroll Wood in the hall. And he said, "It won't work; we won't allow it. If you get a good grade in this course, we won't allow it. It's unfair. You are Professor Fernald's 'apple-polisher'." (laughter). Not understanding the significance of "an apple-polisher" in American schools, I replied, "No, I didn't polish his apples; he had no apples. I gave them to him."

Fernald liked to alert his students before starting classes. One day, as we all gathered around him, instead of opening his book he put his hand on his bald head and said, "I forgot where we stopped. What shall I talk about?" Well, immediately I picked up. I said, "What about continuing the last chapter of the Book of Revelations, Professor Fernald?" (laughter). I think that it must be because of this comment that he gave me a passing mark (laughter). We all had fun with Professor Fernald. Thank you. (Applause).

R. A. HOWARD: For many years, all of Professor Fernald's graduate students were required to take on as a thesis, a topic that was associated with the development of *Gray's Manual.* I think one of the first people to violate that particular edict was Walter Hodge, who somehow got some work in on the flora of Dominica, but he was such a master photographer that, I think, Fernald admired the technique of what he was doing, and Fernald certainly used many of Walter's pictures in the course of various publications. Dr. Walter Hodge joined the Club in 1939. He now spends his time partly in Florida and partly down on the Cape, and he is here this evening with Barbara. Walter, will you talk?

WALTER H. HODGE: Thank you, Dick. Yes. I'm pleased to be here, also, to participate in this tribute to Merritt Lyndon Fernald. As Dick Howard just alluded to, I hadn't realized that I was one of the odd-balls who didn't pick up a thesis topic dealing with the *Gray's Manual* range. It so happened that I had been studying or working at Massachusetts State College, now the University of Massachusetts at Amherst where I was a young instructor. My former professor at Clark University, where I did my undergraduate work, was David Potter, another Fernald student; and it was through David Potter that I got to know Fernald and also the reason I was up at Mass. State, which was Potter's Alma Mater. Anyway, while at the State College, I became interested in the tropics; I was starting a course in an area where I eventually became very much interested, Economic Botany, and I wanted to make a trip into the New World tropics to collect economic plant specimens for teaching purposes and so forth, and perhaps identify a doctoral thesis problem. And so it happened, as Dick Howard has said, that in 1937 I spent a couple of weeks on Dominica, then a British island. Since it was little known botanically, as most of the Caribbean islands were at that time, I had to visit the Gray Herbarium in order to identify what I had collected. And in the course of this, I met up with Fernald. I had been told earlier up at Amherst, "Well, young man, you're an instructor here, but you ought to go on and get a doctorate." That I well knew, so I broached the subject to Fernald, stating that I had what I thought would be an interesting thesis problem for me, a floristic study in the Lesser Antilles. Well, he hemmed and he hawed and, as I recall, he snorted about the botanists down in Washington who spent most of their time in the tropics when they didn't know a darn plant around the Washington, D.C. area, where he was picking up novelties all the time. He and Bayard Long were then collecting in eastern Virginia. Fernald had had some physical problems and wasn't able to continue "the more rigorous field work," up in the northeastern area, so he was "graduating" to the flat coastal plain area of Virginia.

Anyway, he couldn't understand why I couldn't find a problem in that area, or at least in the *Gray's Manual* range. But I said, "Well, I really hoped I could do something in the tropics. I have been teaching, Professor Fernald, up at the State College and I also do photographic work, which I enjoy as an avocation." This brightened his eyes a bit. It happened that it was a rather fortuitous time because Eugene Ogden, who is here tonight, was just finishing up his thesis work and he had been doing the photographic lab work and assisting in Fernald's courses and so Fernald needed a replacement and I guess he sort of said to himself, "Well, anyway, I'll get the photography and the teaching done, even though Hodge doesn't elect a thesis problem that focuses on the *Gray's Manual* range." So that's how it happened that, as Dick says, perhaps I broke what had been a general precept to work under Fernald. Well, in a way, that was a relief for oftentimes I didn't get bogged down when Fernald would come around, as he was wont to do, reading his own manuscripts on coastal plain plants for the *Contributions* or for *Rhodora,* or what-have-you, and if I had a lot of things to do, well, I could always say, "Well, Professor Fernald, there are some prints washing down in the darkroom. I really must get down to them." So he would rush around to find someone else more appropriate to whom he could read the manuscript.

In those days, from '38 to '41, among student confreres at the Gray were Reed Rollins, Rolla Tryon, Bob Godfrey (too bad he isn't here; he'd have some great tales to tell), Jim Soper, Shirley Gale (now Shirley Gale Cross) and Bernice Schubert. Of course Reed Rollins had been around a year or two before us, as had Louis Wheeler as well. I forget who else was there; oh, yes, Carlos Muñoz, a Guggenheim Fellow from Chile, with whom we had great fun. Well, I recall, as others do here, that the most fun with Fernald was when he was in the field. Although his lectures were full of all sorts of interesting stories, he really blossomed when he went into the field. Of course the trips in what we called Biology 17, down on Cape Cod were the greatest time for most of our fun. Invariably Fernald would rent, as Reed has said, a house and then we'd go out into the field and that was a time when we learned among other things about some of the materials that appear in *Edible Plants of Eastern North America.* For example, I can recall that we tasted for the first time the fresh shoots of orach, and the tubers of *Stachys,* and once when Professor Fernald was explaining something, one of us slipped a plant into the band of his fedora. It really wasn't a *Solidago,* Reed, as I recall, it was something more appropriate. It was a stalk of *Lespedeza capitata;* and all the while he went right on telling us about the differences between this and that plant.

One of the interesting times on these trips were the evenings. Then he would reminisce about former field experiences. I'm sure some of you must have heard, this being the Cape, of one of his famous problems with the local police during World War I. You know Professor Fernald looked sort of like a little Prussian with a goatee and while in the field he would be dressed as a European might be with a suitcoat and a tie, no loose sport shirt or anything like that, and an old felt hat. Well, on this occasion he was looking for *Orontium aquaticum*, the golden club, which had a northernmost extension somewhere on the Cape. In order to locate this plant, he went to one of the fire towers on the Cape and got out his fieldglasses ("spy-glasses"). He was equipped of course with a vasculum—a "bomb-case," and as it turned out, he had a little "code book" as well, which was a *Gray's Manual* check-list. To the police he was reported to be a spy trying to help German submarine captains, presumably cruising offshore. Anyway, he was put in jail (laughter), and only after a call was made to Harvard's President Elliot was he released. He was a German spy! (laughter). I think the same thing happened during World War II in a Virginia railroad yard, but I don't recall the details.

One of the other stories that came out on one of those field trips had to do with Fernald's excursions on the Gaspé with Professor Pease. I had spent some time in the Shickshocks, in Fernald's nunatak areas, and so was particularly taken with his stories of how he and Pease first tried to navigate along the Gaspé coast. That was before there was any highway, so they traveled down the St. Lawrence by fishing boat, I believe, from village to village. On one such occasion headed for the Shickshocks, they were unable to find any overnight accommodations. As it turned out, they went to the local post office, which was just a little frame shack with a door opening directly onto the street, and asked the local postmaster what he could do to help them. His reply was, "Well, there isn't any place where you can stay around here, but I'll tell you what. Why don't you just spend the night here in the post office. Of course, I'll have to lock you in, but I'm here promptly in the morning." They said that was fine, and it was so arranged. But pretty soon after they were locked in and it was time for putting down the bedrolls, one of the "urges" came along and they wondered "Well, what the heck are we going to do?" I don't know who it was, Fernald or Pease—probably it was Pease (laughter)—who said, "Well, Fernald, there's the mail slot!" (laughter). On the same trip, they were up in the Shickshocks. Pease, Latin scholar, said one day, "Have you noticed, Lyndon" (or Merritt, or whatever he called him), "what we're using here for T-P? It's quite appropriate—*Dryas*." (laughter). Fernald enjoyed these earthy stories, and whenever he was getting a point across, people may recall that he hit his forehead like this (with the heel of his palm), whether he was reading manuscripts or what-have-you, and that was to emphasize the point.

Well, I think that is the last anecdote that I should tell. However, I do recall that the war came on rather promptly after I left Cambridge in 1941 and many became involved in the war effort. I was abroad for several years and didn't see Fernald until my return from Peru. We had been using alcohol in collecting herbarium specimens of *Cinchona* in the Andes simply because it was a little easier then using presses. I hadn't seen any published record of this, so I wrote a short article for *Rhodora* to report on it. I think Dick Schultes urged me to do this. He'd been doing something similar utilizing formaldehyde. Anyway, I wrote this piece and I got a nice reply, the last letter I received from Professor Fernald, written to me at M.S.C. (Amherst) in April of 1947:

> Dear Hodge: At the risk of making *Rhodora* seem to some readers to be a saturated solution of preservatives, we shall be very glad to use your fine paper later in the year. I am glad that my work has been in temperate regions where it has not been necessary to smell of alcohol (laughter). Kind regards to the Mrs. and the youngster. Yours sincerely, Fernald, Editor-in-Chief.

Thank you. (Applause).

R. A. Howard: We could get started on the Hodge-Godfrey stories around here, too, but one of them involved the time when we were in Cuba and Bob Godfrey knew that Bernice Schubert was working on the genus *Desmodium*—*Desmodium* has adherent loments, you know, that stick to your socks—and so after one day in the field, when we came back with a set of socks that were just loaded up with these fruits, Bob Godfrey decided that this was the thing to send to Bernice Schubert, so he mailed them up to Cambridge and the post office and the Harvard Herbarium were never the same after that! Bernice Schubert was one of the key people in Fernald's production of *Gray's Manual* the 8th edition. We hoped that she would be here tonight. Unfortunately, she was not up to it today. I just want to read the last bit of the Preface of the 8th Edition that Fernald wrote:

> Finally, especially since the impairment of his eyesight, the author has had the most loyal, conscientious and unlimited aid of Dr. Schubert in the exacting details of coordinating usages in the text, editing the manuscript for the printer, checking and double-checking the citations of figures, and in

> the scores of other details necessary in the book as it goes to press. My appreciation of all her helpfulness cannot be adequately expressed.

If you read a lot of Fernald's writing, you will never again find a dedication that is as warm as that or as sincere as that, so we felt that Bernice could contribute something to this program. She has indeed supplied a few of her letters, and while we are going to ask Dr. Carroll Wood to talk anyway, he is going to represent Bernice Schubert, too, at the microphone. Carroll.

CARROLL WOOD: Well, Bernice was unable to be here tonight. She has been having some difficulty with a respiratory problem and she said she just couldn't make it. But she did agree to write down a few things. She felt very warmly toward Professor Fernald and he toward her, and I think she was reluctant to talk about him very much in public, but she did look into her file of letters from him and we've got some quotations from those. She writes:

"I'm sorry I can't be present at the meeting this evening, but most of you know that I worked rather closely with Professor Fernald, especially in his last years of effort on the 8th edition of *Gray's Manual.* Most of you are also aware of his botanical accomplishments and are familiar too with one aspect or another of the mythology that has grown up around him. I should like to have you know a little of how I felt about him as a person, as a teacher, and as the person for whom and with whom I worked at the start of my botanical career. I wondered for some time about the best way to present a few ideas and remembered a folder of letters from Professor Fernald to me on two European trips when I photographed type specimens for him. Perhaps just a few excerpts will acquaint you with him best. However, as an introduction to Merritt L. Fernald, a few lines written in 1891 by his mother to Sereno Watson, then Curator of the herbarium, may serve. Mrs. Fernald writes:

> I write to ask you not to hold our son Merritt responsible for the false and senseless reports which have in some manner found their way into the daily papers, regarding him and his going to work in the Harvard Herbarium. It is a matter of great annoyance to us all and especially to Merritt, who is a very modest and diffident boy. As the simple statement about his leaving home, which we have made when necessary and desirable, added to certain mistaken and exaggerated notions

> expressed by some of his college mates, have in some way furnished material for sensational reporters. Of course, we are doing what we can to correct false impressions. And Merritt's disgusted exclamation, "What will Dr. Watson think of me?!" made me wish to set the matter right with you at once."

This is from a letter in the Gray Herbarium archives, and apparently newspapers had picked up this sensational thing about the young boy from Maine going to become a professor at Harvard. Bernice continues:

"On the day that World War II ended in 1945, Professor Fernald suggested that I look into the possibility of going abroad to study and photograph type specimens for him. In late October 1946, I managed to get off on my first trip outside the United States. On arriving at the British Museum (Natural History), I found a letter with a note from Professor Fernald:

> To greet you at the herbarium at South Kensington where I spent very happy weeks in August and September, 1903, and again in the summer of 1930. You will find the botanists there a very kind and helpful group. We are imagining you toasting along the Gulf Stream today and very soon steaming into the Channel.

"His note was followed by notes from several members of the staff. By mid-November, many new botanical requests started to come in the letters:

> One item has just come up. Please make a note of the degree of pubescence on the leaves of *Fraxinus caroliniana* Miller. Ordinarily, *F. carol.* has been treated as the glabrous-leaved tree and the pubescent one called a var., but Miller says it is pubescent. Sargent and others, including me, seem to have taken it for granted without going back to Miller. Foster and I are reading the *Manual* transcript for an hour daily, checking for consistency in small details. He is a great help, catching errors of centimeters for millimeters, and so forth. Pease has finished checking the Latin and Greek except for recent manuscript, and I shall say in the preface, 'if any errors are found, they are obviously of sections we did not see!'

"Often there were snippets of news or gossip that followed requests, as in the following letter of late December 1946:

> Here is another type in the Linnaean Herbarium. Do find out why the Linnean Society 'with an E' but Linnaean Herbarium 'with an AE'. Weatherby asked, I too, that you examine a photograph, and photograph with details of the lower leaf surface of flowers, if possible, to determine whether the leaflets are pubescent beneath, in which case, *T* (which is *Thalictrum*) *purpuream* displaces *Thalictrum polygamum* Muhl. or, are they covered with waxy atoms in which case it displaces *T. revolutum* D.C. Incidentally, Boivin is bringing down to the meetings after Christmas a 'young bride,' Cousette Marcou, director of the Children's Gardens at the Montreal Botanical Garden. Cousette sounds rather cuddly (laughter).

"The last letter I received during this trip was in January 1947 and contained a rather detailed description of the Triple-A. S. meeting held in Boston in December along with a plaintive note, saying that he hoped I would be back soon to help him clear his table and clean his 'specs', which no one had done in my absence.

"In the spring of 1950, I was fortunate to be able to go abroad again to travel to more herbaria, to attend the first International Botanical Congress after the war, to do some of my own research, and to fill some more requests for Professor Fernald. Several members of the staff, including Professor Fernald, saw me off, and not long after my arrival in London, I received a letter with botanical requests concerning *Spiranthes* and the following paragraph:

> We were delighted to know from Miss Campbell that you had a good trip. With blizzards and shipwrecks along our coast, and the long delay in receiving your manuscript, we pictured you as being like the heroine of my youth:
>
> 'To sail out on a broad ocean,
> A sweet little maid took a notion.
> But when the yacht rolled,
> She said, "I'd give gold
> To get rid of this horrible motion".'
>
> and there's more:
>
> 'There was a young man from Ostend
> Who vowed he'd hold out for the end.
> But when halfway over
> From Calais to Dover,
> He did what he didn't intend.' (laughter).

"He also mentioned in this letter that he had received proofs up to page 1500 of the new Manual. Letters continued to come, but shorter and mostly dictated, because during this period, he had a coronary thrombosis and although he returned as soon as possible, by stages, to working, it was difficult, as his eyesight had been somewhat affected. However, he did see his Manual, he enjoyed and appreciated the letters he received from all over commenting on it, and I think he felt he had completed this work to the extent of his ability. Surely this meeting is proof that he produced something of value and that his influence still lives."

And these are some comments by Bernice Schubert, whom I first met when I came to Harvard as an ex-G.I. in 1946 by virtue of the G.I. Bill. I had corresponded with Fernald earlier from Virginia where I was collecting plants. I had gotten interested in taxonomy through a student of Fernald's, Jack Fogg, who at that time was a professor at the University of Pennsylvania. I had intended to go back there after the war, but when the opportunity came, I thought, "Well, Professor Fernald is the one that I ought really to go to work with," and so, with Fogg's blessing, I wrote to Fernald, and somehow he got me into Harvard in the middle of the summer of 1946. As Dr. Hu has said, we were both in that last class he taught in the spring of 1947. I remember a couple of the stories she told, and "The Last Chapter of Revelations" has always been one of my favorite ones, because it was quite appropriate. The first half of his course with the autograph collection was fascinating. As she said, he only got about half-way through the alphabet, but I think he did get as far as Marcus E. Jones; and he even pointed out the scurrilous attack that Jones had made in print on Fernald himself, along with a lot of other people. The second part of the course was mostly readings from the geographical papers of Fernald, and most of us had read these. That day when he came in, as I recall, he had a volume of *Rhodora* open and he said he didn't know quite what he was going to use as a text for the day, and she remarked, "How about the last chapter of Revelations?" Everyone laughed and Professor Fernald got what my mother calls "the dry grins," which is when the joke is on you, you *have* to laugh, but you don't really want to. For years, I wondered whether Shiu Ying really knew what she said then.

Fernald's habit of reading to people was notorious. I got cornered numerous times with that. You couldn't get away once he was reading, and usually these were manuscripts that he later published in *Rhodora.* It was a long time later that I realized that he wasn't really reading to the person in front of him. He was reading to himself. He was polishing his prose, and of course one of the best ways to do that is to read the terrible stuff you've written out loud to see how it sounds. A story that Professor Raup told me illustrates this very nicely.

Dr. Raup has sent two pages of newsprint, which are typical Fernald manuscripts (he has saved them all these years and sent them to Dr. Howard) in Fernald's handwriting, which never changed at all throughout his entire life, as far as I can see, which makes it very difficult to date his annotations in the herbarium, which he frequently forgot to date himself. But Professor Raup told me that one Saturday afternoon he came into the Gray Herbarium to do some work and brought with him his little boy, only three or four years old. Along came Professor Fernald who started to read to them. The little boy was sitting on the table and was fascinated by Professor Fernald's goatee (laughter) as it went up and down as he read. Raup stood around for a few minutes, then he went off and did what he had to do in the herbarium; when he returned 45 minutes later, Professor Fernald was still reading to the little boy (laughter) who was listening attentively, so it was evident to whom he really was reading!

Well, the hour grows late. I've been reminded of all sorts of things that I had forgotten all about, including the lunch and the carrot in the Radcliffe room. It was there that Professor Fernald, who was very kind, showed me about eating the flower buds of *Hemerocallis* (daylilies) which he had cooked in a custard. He had a little jar of those one day and tried it out on me. He also pointed out to me the new shoots of *Polygonum cuspidatum* which he said made an interesting "nibble." I tried those and, after reading *The Edible Wild Plants of Eastern Northern America,* I eventually decided that anything Professor Fernald said was a "nibble" was inedible to anybody else but him (laughter). He was willing to try anything. That's where I think I'll stop. Thank you. (Applause).

R. A. HOWARD: We've all known about the manuscripts that Fernald used and read to so many people. It was an unsized half-a-sheet of newspaper, and it was read over and over again. My favorite story about this concerned the time when Munroe Birdsey, whom some of you may know, came into the Gray Herbarium for the first time. In the corner at the side of the door was a mail shelf which was just high enough to hit Birdsey in about the back of the neck. As he walked in (I was up in the second balcony so I heard all this going on), Fernald, who usually shuffled his chair as he pushed it back, cleared his throat—chmmm—and it was time, obviously, that somebody was going to be "read to." Birdsey came in the front door, just as Professor Fernald came into the atrium there. There was no one in sight, and Fernald looked up at Birdsey and said, "I think you would be interested in this," and then proceeded to read. About 20 minutes later, he looked again at Birdsey and said, "What do you think of that?" and Birdsey said, "Well, that's very interesting, sir, but who are you?" (laughter) and Fernald said, "M. L. Fernald." And Birdsey said, "Not *the* M. L. Fernald?!" In the meantime, he had been backed up against the mail shelf so that his neck was almost broken, but he tells the story on himself, too. That was his introduction to M. L. Fernald. Those sheets are very, very rare and we literally could not find any around the building. There may be some in the archives, but when I mentioned this to Professor Raup, he discovered in his old manuscript that he published on the Peace River flora, that he still had a sheet which was Fernald's description of an *Antennaria* published in that particular *Contribution* of the Arnold Arboretum.

Being the last speaker in one of these series is the most difficult because the best stories have been told and probably everything you had to say has been said in one fashion or another, but we asked Dr. Richard Schultes to give us some of his recollections of M. L. Fernald. Dick.

RICHARD EVANS SCHULTES: Sorry, I'm just back from Borneo with a jet lag, so I'll have to follow notes.

Whenever former students of Professor Fernald get together, the tales inevitably flow endlessly throughout the evening. Fernald, irritating but lovable, was truly what is generally known as a "character," of which Harvard in those years had an ample share. I don't think there are any around now (laughter).

But Fernald never shrank from a fight. It did not matter whether the opposition was a colleague at Harvard, a botanist somewhere else who dared to disagree with him on a matter of taxonomy, or even the University administration itself. His typically Maine straightforwardness and bluntness came to the fore. In the several courses that I took with Fernald as an undergraduate and graduate student, I came to respect "the Prof" for his incredible knowledge of the temperate American flora, for his extraordinary understanding of the historical development of North American botany, and for his natural ability as a teacher, and yes, even for his occasionally irascible reactions. In those years, the three dominant figures in Harvard taxonomic botany were Fernald, Elmer D. Merrill, both State of Mainers, and Oakes Ames, a Bostonian. Although he held both Merrill and Ames in great respect as botanists, Fernald enjoyed piquing both. Merrill always responded, which is exactly what Fernald wanted. Ames, always aloof, never rose to the bait, which infuriated Fernald (laughter).

It is said that Fernald sometimes made it difficult at the Gray Herbarium for students of other professors, especially those professors with whom he was carrying on a scrap. I was doing my graduate work under Ames, but Fernald always treated me courteously, even in a fatherly way, as if I were one of his own students. Only once did I personally sense his antipathy towards Ames. Whilst preparing for my first collecting trip to southern Mexico, I asked Fernald if I might look for any material for him. He asked, "Schultes, how many corrugated cardboards are you taking?" When I replied that I was not taking any cardboard but aluminum corrugates because I would be working in the wet tropics, his eyes sparkled and he remarked, "Oh, yes, I forgot. You work with that rich dilettante down in the Botanical Museum" (laughter). He said, "We at the Gray Herbarium cannot afford such a luxury as aluminum corrugates!"

How well I recall the many interesting quips and jabs that often served to impress upon us some important point in the mass of details that without a single note he poured forth in lecture after lecture. His characterizations of other botanists from Linnaeus to his contemporaries was telling. For example, he described a taxonomist whose treatment of the Cyperaceae left much to be desired as a "bombastic boob." He consistently referred to the great botanist, Liberty Hyde Bailey, whom he respected highly, as "free-skin Bailey." He carried on, in the pages of *Rhodora* which he edited, a spirited fight with Gleason of the New York Botanical Garden on the classification of raspberries, finally adding to one of Gleason's own papers in *Rhodora* a footnote to the effect that he would no longer try to set Gleason right because he did not have any time for "more Bronxian sophistries."

His lectures were unorthodox to say the least, interspersed with constant references to piles of herbarium specimens. He had mannerisms which he used as punctuation for his lecturing. Rising on his toes, for example, meant special emphasis—"italics," if you will. Stretching out both hands, palms upward, meant a question mark. A vigorous slap on his bald head was an exclamation point. But perhaps the idiosyncracy that I most vividly remember about this outstanding teacher and botanist was his method of writing and editing his own papers. He wrote always, seated at a desk in the public part of the library and not in his own office, if indeed he had one. He used a thick carpenter's pencil and long sheets of plant collecting paper. Insertions, corrections, arrows for additional paragraphs, scratched-out phrases all of this was such a mess that only one secretary who had typed his material for years could decipher the manuscript.

He always wore thick heavy-duty shoes. Often, when an unsuspecting graduate student would pass by, out from under Fernald's table would come a leg. The heavily shod foot would stamp on the floor, there would be a clearing of the throat, and Fernald would say, "Well, Schultes, what do you think of this?" He would then read the whole manuscript in the greatest detail to the trapped student, adding copious ad-lib explanations, stopping to write in corrections, add or delete phrases. He thoroughly enjoyed this pastime and interspersed his reading with an occasional chuckle of satisfaction. And I must say that, while at the time we all thought that it was an imposition on Fernald's part to trespass on what we thought was our valuable time, I realize how much botanical material I learned and how much I absorbed about writing manuscripts from this unusual custom.

Now, before ending these reminiscences that could go on and on and on, I must mention Fernald's field trips. They were superb, but there is one in particular that I will never forget. On one Saturday in late October, we were to drive to the tip of Cape Cod. We would stay overnight in Provincetown in a beach house, and Fernald told us not to take any food for he would cook up a dinner of clams and beach spinach. I had offered to drive. The day dawned with torrential winds and rains, the backlash of a hurricane. Cambridge streets were deep with water; branches of trees were falling. Elso Barghoorn, who was to ride with me, was certain that the trip would be postponed. When we arrived at the Herbarium, Elso suggestively volunteered to Fernald that "it was raining" (laughter). But Fernald chuckled and replied, "Well, the plants are still there, aren't they?" And we all went. But since we had had a frost, I felt that our chances of collecting sea spinach were not too bright, so I bought and secreted in the glove compartment several chocolate bars just in case of an emergency. We did find sea spinach but all the leaves had fallen off. Undaunted, Fernald collected an armful, proceeded to boil it and serve it, stuffing the twigs into his mouth and trying to convince all of us that it was a delicious repast (laughter). But, before going to bed that evening, I sneaked out to the car and devoured several chocolate bars. Fernald never knew how little I appreciated his economic botany on that trip! (laughter).

Over the years, I have at so many times realized how fortunate I was to have Merritt Fernald as a teacher and to have studied with him. I'm glad that in this 800th meeting of the New England Botanical Club, of which he was such a dynamo, some of us who were so fortunate have shared with all of you what we remember of our days with, and exposure to, this great giant of North American botany.

R. A. HOWARD: Thank you very much, Dick. I am sure these stories have brought to mind others that some of you have. For those of you who have sent material in to us, add to it, if you come to the thoughts. The hour is late so we won't ask for more contributions now. We intended this program as a tribute to M. L. Fernald. As I said at the beginning, I hope those of you who did not know him, to whom he is only a name, have gathered from our comments that he was really quite a person. Thank you very much.

MARY WALKER: Back in the Council minutes of late 1982, early 1983, there used to appear, "The 800th meeting is coming in May 1984. Are we going to do anything about it?" Thanks to the efforts of Garrett Crow, who has done a lot of the organization, and to Dr. Howard, who has been a wonderful Master of Ceremonies, and to all of our speakers who've given us this picture of Fernald, I think we *have* done something about it. So, I wish to thank you all once more.

May I have a motion to adjourn the 800th meeting?

[It was so moved, at 11:25 p.m. Ed.]

LETTERS AND EXCERPTS ALSO RECEIVED FOR THE "TRIBUTE TO FERNALD" EVENING

from Ernst C. Abbe:

As I look back on that golden age of graduate work at Harvard in the '30's, I well remember my desire to do well in Fernald's eyes and the strange twist of fate which led me to differ with him so profoundly. Although my main concern was morphology, I was drawn to the Gray repeatedly from 1930 to 1949.

The number of anecdotes growing out of those years is endless and each one illuminates another facet of Fernald's complex and charismatic personality which tolerated no neutral onlookers; it seems that all who were associated with him developed a love-hate relationship. For instance, his sturdy New England egalitarianism is so well illustrated by his response to Ms. McKelvey's complaint that she had to sleep under the same roof as her chauffeur on the Cape Cod field trip in the fall of 1930. Fernald's answer was that not only would he not hesitate to sleep under the same roof but would even sleep in the same bed with her chauffeur if necessary, thus leaving Ms. McKelvey to decide to what extent she might wish to emulate Fernald in this specific instance. Then there was the enormous scorn he could heap on an opponent as in the case of Professor Jeffrey's "absent treatment hybrids" whose parent species were so far apart that it would take several relays of devoted bees to effect cross-pollination. Or his absolute fairness in sponsoring my Guggenheim even though he knew that my collections represented a test of his cherished Persistence Theory. Nor will I forget my surprise when he upbraided me after our return from Virginia for having persuaded him to buy a Virginia "peanut-fed" ham which had ruined his reputation as a cook because it retained its mahogany-like consistency after hours of cooking.

Fernald's violent reaction to the manuscript of my paper on northeastern Labrador was the only really traumatic experience I had with him, but it could not be avoided—and because I valued his good opinion it was profoundly disruptive of my peace of mind and diverted my activities for several years from my major area of research. Also, a third-hand version of the affair has appeared briefly in print so that perhaps a first-hand account is in order.

It all centered around Fernald's Persistence Theory of which I first heard in Wiegand's taxonomy seminar at Cornell in which it was treated as revealed truth and accepted by me as such. So when Fernald held forth on it after I went to Harvard, I nodded my head sagely and continued to accept it without question. At this time Alexander Forbes of the Naushon Forbeses and the Harvard Medical School asked Fernald to send one of his students on Forbes' expedition to Northern Labrador, provided such a student had a strong back and could handle the ropes on the expedition's Lunenburg schooner; Fernald recommended me. Fernald told me he wanted me to go because of my previous collecting experience on the North Shore of the Gulf of St. Lawrence and because he wanted me to get as many collections as possible from the tops of the Torngat and Kaumajet Mountains which he was convinced were former nunataks and should have many "relicts" waiting to be collected. He felt that there was an excellent chance of getting to such nunatak areas because the famous mountain climber and glacial geologist Noel Odell was to be a member of Forbes' expedition and had specifically asked Forbes to add one of Fernald's students to the personnel of the expedition. Fernald pointed out to me that his graduate students could not spare the time from their monographic work to do floristic work of this sort, but that he would like to have me serve as botanist on the expedition. I happily agreed to go and was vastly flattered in the bargain, although I disliked heights and mountain climbing; by following closely in the footsteps of Odell, I climbed a number of mountains in northeastern Labrador. But on mountaintop after mountaintop the plants turned out to be the ubiquitous arctic species, not the "relicts" that were expected. It was at the lower elevations where moisture and rock type were favorable that the significant rarities occurred. To add to my disillusionment, Odell was convinced on geological grounds that the highest peaks had been ice-covered so that there could not have been any nunataks where "relicts" could have survived. In my opinion even if there had been nunataks, the conditions would have been so inhospitable that only the hardiest plants could have lived on them, and that it was the ice-free forelands, if any existed, which might have supported the rarer plants. Yet here again Odell felt that such areas had not existed. If Odell's views were to be accepted, only one conclusion was possible; every species, "depauperate relicts" included, had to have migrated into the area in post-glacial time—all of these views were sure to be abhorrent to Fernald, especially the last. Yet I could not, in all honesty, avoid these conclusions. Various good reasons prevented a confrontation at this time a summer in northern British Columbia with the Raups, intensive work on my thesis with Wetmore, an NRC post-doc at Columbia with Sinnott. The latter worked out such that I was able to spend the spring of 1935 at Harvard again and concentrate on writing up the Torngat paper, the painful typing of which I completed just before leaving for the University of Minnesota.

I took the finished manuscript of the Torngat paper to Fernald in mid-afternoon the day before we were to leave town. Fernald sat down with me at one of the tables in the library of the old Gray on Garden Street and looked over the illustrations, which he liked, and then began to read the manuscript about which he was enthusiastic, -- at first. In fact, he went off and found Weatherby somewhere and read excerpts to him and said, "This has to be published as a *Contribution,*" whereupon Weatherby beamed benignly, and went on his way. The afternoon wore along, Miss Sanderson left, and soon Fernald and I were alone and nearly through with the manuscript. At this time Fernald came to the discussion summarized above and immediately began to fulminate. He brought up all the information and arguments that he had so carefully worked out for the "Persistence" monograph and subsequent papers. The vast mass of detail, the irrefutable logic were overwhelming, but I told him I could not accept an extension of his conclusions to the area I was familiar with, and furthermore Odell's independent conclusions about the glacial geology fortified my views. Fernald demanded an explanation of what kind of an authority this man Odell might be, what did he know about *roches moutounees,* etc., etc. I pointed out that I had allowed for Odell's interpretation being incorrect and that even if there had been nunataks, etc., I was driven to conclude, against all my earlier preconceptions, that the Persistence Theory was inadequate, that there had to be extensive post-glacial migrations. Fernald stated that as Editor-in-Chief of *Rhodora* it was one of his perquisites to insert footnotes wherever he considered that the text of a paper needed correction. I agreed, but stated, perhaps a bit coldly, that as a member of the New England Botanical Club it was my privilege to submit the manuscript for publication (in retrospect, a rather weak rejoinder on my part!). Fernald conceded this point and then launched into a thorough dissection of my personality (always had been a bumptious person ever since I first came to Harvard, etc.). His enthusiasm mounted with this sally and he recalled having known my father (Harvard, 1894) and proceeded to dissect father's character, scattered it in bits on the floor of the library and figuratively did an Indian dance on the quivering remains. Finally he did the same for my grandfather (Harvard, 1864) which showed a high degree of ingenuity, because my grandfather was at Harvard roughly thirty years before Fernald came as a student! While I was pointing out that such character analysis has no bearing on the matter under discussion, the phone rang. It was Fernald's daughter reminding him that it was 7:30, dinner was getting cold, and should she hold it any longer? Whereupon Fernald took the manuscript and left for home without a fare-you-well! I was exhausted and furious.

The subsequent events have always amazed me; in retrospect I feel that Weatherby as usual had an ameliorating effect on Fernald's often drastic inclinations. For, a few weeks after I arrived in Minnesota, I received a very moderate letter from Fernald as Editor of *Rhodora* saying he would publish the paper and recommending that I change "northern Labrador" to "northeastern Labrador" in a number of places in the text. Then, to my vast surprise, he published it as a *Contribution*!

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from George L. Church:

A man with a spring in his step and a lively manner entered the laboratory and proceeded briskly to make the pile of herbarium specimens before him seem to come alive. Indeed, as I listened to Professor Fernald in his class in 1925, he was unfolding a vivid picture of the natural community in which each specimen had been collected. Furthermore, I soon realized that the enthusiasm in his discourse had been well nurtured by more than three decades of meticulous studies of plant populations in a host of areas in New England and eastern Canada.

As I delved into the early volumes of *Rhodora*, I continued to be enthused with Fernald in the accounts of his many expeditions to such alluring natural areas as the St. John river drainage system, the Matapedia Valley, or the Gaspé Peninsula. A few years later, when I myself had the opportunity to visit some of these choice collecting places, I felt as though I had really been there earlier with M. L. F.

Although we were left to our own devices in laboratory study, we were always free to interrupt Fernald for consultation in the Herbarium library where we found him vigorously writing. Before answering a question, he would often look up over his half-frame spectacles and say, "Listen to this!" I recall particularly the time when the well known volume entitled "Age and Area" by Willis appeared. With a wealth of knowledge of the flora of unglaciated North America, Fernald could easily refute Willis' theory that the oldest species had the widest geographical range. I can still hear him exclaim gleefully as he looked up at us again after his demolition of Willis,—"Willis should have called his work AGE AND ERROR!"

In 1925, the New England Botanical Club used to meet in the imposing building of the American Academy of Arts and Sciences on Newbury Street in Boston. It was at the monthly meetings there that I enjoyed Fernald at his best as a colorful raconteur. With great delight, he would relate his experience as a camper, mountain climber, and collector in Maine or the Maritime Provinces. He took great pride in his ability to explore an area in spite of such interferences as the ubiquitous, invisible mosquitoes of the northern woodlands or the wild dog packs of the serpentine barrens of Newfoundland.

Certainly, hazards of field work in no way impeded Fernald in pursuit of adequate data in support of his well known concepts of distribution.

In fact, whenever I recognize herbarium specimens bearing annotations in a clear, bold handwriting with the initials M. L. F., I relive the excitement of following a trail blazed by Merritt Lyndon Fernald.

from Lincoln Constance:

Out of the sea of recollections of Fernald that come back to me, I shall confine myself to three.

I first visited Cambridge in 1942, just after Reed Rollins had accepted an appointment to the faculty of Stanford University, and asked Professor Fernald if he was not as greatly pleased as I was. He looked at me quizzically for a moment and then snapped, "They're pretty radical out there!" So much for Clausen, Keck and Hiesey, and what Stafleu calls "the Birth of Biosystematics. . . ."

Sometime during my stay, I encountered a letter Fernald had written to one of his cronies (perhaps Bayard Long?), complaining that one of Fernald's students had been required to take a course in Physiology, "Whereas you and I know that the best training for a taxonomist is a thorough grounding in Latin."

At Fernald's request, a meeting was held in the Director's office with officials of the America Book Company, a representative from the Harvard Treasurer's office, Professor I. W. Bailey and myself, to see if we could speed up completion and publication of the *Manual.* I told the group that so far as I could tell, the ms. had reached the point where commencing to print the first part would ensure prompt completion of the remainder, and it seemed that the company would be agreeable to this interpretation. At this point, however, all other considerations became secondary to the somewhat complicated question of royalties. The company representative professed to be overwhelmed by what he regarded as Fernald's exorbitant demands, and asked if he might smoke. Fernald, a vociferous anti-tobacconist, was more than agreeable. I'm not sure whether he got up and lighted the gentleman's cigar, or did I only imagine it? (The "agreement" came unstuck and Reed had to renegotiate it a few years later).

Finally, I had a story from Henry A. Gleason, who visited Cambridge that year to serve on an appointment committee. He related that when he visited Elmer D. Merrill at the Arboretum, Merrill was chuckling and said, "You remember that row of moth-eaten, broken-down elms around the Gray Herbarium? I had them cut down!" When Gleason called on Fernald, he was fuming, "Do you know what that fool Merrill did? He cut down the elms that Asa Gray planted!"

from William B. Drew:

I first met Prof. Fernald in the fall of 1930 when I enrolled in Botany 7. At that time Botany met in the so-called Harvard Room, a classroom in the Gray Herbarium. Prof. Fernald entered the room, his beard neatly trimmed, and proceeded to begin his lecture with the gymnosperms. Those of you who took his course may recall that it was largely based upon a key to the families of the gymnosperms and angiosperms with, of course, frequent references to some genera and species as he went along. He had a very lucid style of lecturing which make for interesting listening. From time to time he told us anecdotes of one sort or another.

One of the stories that was circulating around the Gray Herbarium at that time, I think perhaps told by Prof. Fernald on himself, was that he had never been able to pass an automobile driver's test. He tried it a few times, but apparently went off the road when he saw some interesting plant. He also averred that, as a younger man, or perhaps a youth in Maine, he had tried collecting from a bicycle, and he had a similar fate there. After two or three nasty spills, I guess he probably decided to walk. At any rate, his daughter Katherine was providing the transportation to and from his home and the Gray Herbarium during the '30's when I was associated with him.

Another story, which perhaps may be apocryphal but as far as I know it's true, was told of Dr. Norman C. Fassett, one of Prof. Fernald's outstanding graduates, who was enroute to accept the position at the University of Wisconsin, where he was an outstanding taxonomist. It seems that Dr. Fassett and his family had to be there in a hurry and therefore, with two or more children to cope with, they cut holes in the wooden cover under the seat of the Model T Ford to allow for an essentially nonstop trip, at least as far as the toilet needs of the youngsters were concerned. Later, in 1944, I shared briefly an apartment in Bogota, Colombia, with Dr. Fassett and he indicated that the story was essentially true. Another anecdote about Prof. Dr. Fernald, if it can be called that, was his tendency to be very careful with specimens on display or with any of his large sheets of newsprint on which he wrote in such a beautiful, flowing hand. He felt he had to be careful when certain botanists visited the Gray Herbarium because allegedly at least one botanist had learned through talking with Prof. Fernald, or reading his material, about a new species which he was about to describe.

Apparently his species was scooped by this visiting botanist. So whenever this particular individual, a very prominent botanist of the northeast of North America, visited the Gray Herbarium, Prof. Fernald was always very careful to see that the specimens on which he was working were covered up and his most recent writing hidden under some neighboring papers or specimens.

Another point that I might add was the perspective of Prof. Fernald from the standpoint of a graduate student working under his direction. One had to be very discreet about approaching him, particularly when he was busily writing. I generally found it necessary to make an appointment first thing in the morning when he came in, and then, if I had good luck, I would approach him with whatever material and questions I had in mind at the appointed hour. Usually, if he was really steamed up about a topic, as he frequently was, I listened to his latest writing for a considerable period of time before we got down to cases on my own questions. As a result, I heard a good bit of the linear-leaved North American species of *Potamogeton*, published in 1932, and especially recent discoveries in the Newfoundland flora, published in 1933. Those were interesting papers, but it became a problem sometimes, when I had pressing matters of my own on which I needed answers.

I recall Prof. Fernald in the mid-1940's getting together with Ludlow Griscom, the famous ornithologist, to go over collections they had jointly made in the coastal plain or piedmont of Virginia. They would work over the identifications on which Mr. Griscom was an expert. He was particularly interested, as I recall, in carexes, but he and Prof. Fernald would debate and study the material and reach some conclusion. This usually occured late in an afternoon when Prof. Griscom's work at the museum was done for the day and he came up and worked for an hour or two or more with Prof. Fernald in the main gallery of the Gray Herbarium. The Virginia papers, as far as the coastal plain was concerned, were one paper published in 1937.

Finally, I might add that Prof. Fernald was a marvelous person with whom to go on a field trip, and each spring his Botany 7 class made an expedition to some interesting botanical spot, such as limestone areas in southern Vermont. There we spent a long weekend learning a great deal about the flora of eastern North America and particularly of that region. One other thought occurred to me: Prof. Fernald stood up for his graduate students whenever they became involved with other members of the Harvard graduate faculty. I recall a personal experience when I was invited to present a seminar on my studies of the section *Batrachium* of the genus *Ranunculus* before the group in the Biological Science building. I hadn't told Prof. Fernald that I was going to do this, as I didn't think he would want to be bothered or would have much interest in it. When I presented my paper I discussed at some length the general concept of *Ranunculus* and the subgeneric status of *Batrachium*. This matter intrigued Prof. G. H. Parker, the eminent zoologist, and he gave me a pretty hard time. I was a very callow youth at the time anyway, so I did the best I could, and I think I came fairly close to holding my own. Well, some time later, perhaps the next day, Prof. Fernald accosted me in the Gray Herbarium and said why didn't I tell him I was going to give the seminar? He would have been there to lend me support. Believe me, I appreciated that, so when I had my final oral examination, the committee included Prof. Parker and several other zoologists and botanists; I had no fears about Prof. Parker that time, and much to my astonishment, I finally passed it. Thank you; I hope you'll find this interesting.

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from Joseph Ewan:

What I did not stress in my sketch of Professor Fernald in the *Dictionary of Scientific Biography* is an impression which still persists as a marcescent memory. It is of a large head atop a small man housing a winning epicentricity. On my 1945 visit to the old "Gray" on Garden Street I had sallied forth from a pinched second floor room on Brattle Street to meet in a fertile field, the seat of historic specimens, frames of reference, footnoted by a unique library. Recognizing a willing audience, Fernald led me to an alcove and recommended that I listen to a few paragraphs. Thereupon, with the obvious delight born of years of observing and collecting botanists, he read a critique which was to bloom in the next anthesis of *Rhodora*. Here a Fernald verdict was unabashedly given. Fernald was a holotype. Of quiet but unmistakable speech, he was sincerely interested in the response, especially if it happened to be a contrary view. One was aware that this was Fernald at Harvard, clearly here Fernald was the epicenter.

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from Richard H. Goodwin:

My first encounter with Professor Fernald was when I took Botany 7 with him in my sophomore year in the fall of 1930. The initial lesson was one in local geography, as I arrived breathless at the junction of Garden and Linnaean Streets with enough sweat pouring off my right wrist to make note taking a serious problem. Not being in shape to run a five-minute mile between classes, I managed to borrow a friend's car for the times when I had this tight schedule. Those were the days when one could find a place to park in Cambridge.

The course was filled with graduate students and upperclassmen, who had far more background and maturity than I. Fernald's lectures would frequently begin with a verbal recitation of a section in the "Key to the Families" such as: "e. Flowers unisexual, monoecious, in dense spikes or heads; perianth of hair-like bristles. . . Typhaceae." Then would follow an interesting discourse on the edibility of cattail rootstalks and flowering spikes, or, for the appropriate taxon, a discussion of the phytogeographical implications of its distribution.

Later on, as a graduate student, I signed up for an advanced course with Professor Fernald. I was the only Harvard registrant; there were three from Radcliffe. So, strictly off the record—this was about 1934—the course was given for the four of us, who may have participated in the first "integrated" course at Harvard.

I can remember more than once being cornered in the Herbarium by the Professor who, with sparkling eyes, would try out a draft of his latest manuscript on a willing listener.

In retrospect, Botany 7 and my only too brief contacts with Fernald were highly significant in shaping my career as a botanist. This was surely not due to the very modest amount of information retained from his lectures, nor to the proficiency attained in the use of the drawing pen. Rather, it grew from an intangible attunement to the natural world. Fernald was at his best in the field, and the forays with him to Mt. Equinox and Fairlee, Vermont, and to Cape Cod are still vividly remembered. They were the first of many to follow on my own, and with students and colleagues.

from Hiroshi Hara:

From August 1938 to November 1940, I was a Research Fellow at the Gray Herbarium situated at that time in the Gray Botanic Garden. The main subject of my research was the botanical relationship between Eastern North America and Eastern Asia, which was first pointed out by Prof. A. Gray in 1846, and in which Prof. Fernald was also much interested. I studied mainly under Prof. Fernald at the Gray Herbarium, and also visited the Arnold Arboretum once a week to see specimens and literature there and to talk with Prof. E. D. Merrill and Dr. A. Rehder, both of whom had profound knowledge of Asiatic plants. In those days, Prof. Fernald had been working hard to revise Gray's Manual till late evening, and also preparing additions to the flora of Virginia to be published in *Rhodora*. My room was upstairs, and when I came downstairs in order to check literature at late hours, I often saw Prof. Fernald alone working at his large desk by the side of book-shelves of the library, and heaping up specimens and books high on his desk. So I had chances to talk with Prof. Fernald on various problems. Soon I published a short paper in Rhodora 41: 385 392 (1939). Regarding the Asiatic plants newly found in North America, we intimately collaborated, for example *Cyperus microiria* Steud. by Hara in Rhodora 42: 196 (1940), and *Aneilema Keisak* Hassk. by Fernald in Rhodora 42: 441 (1940).

When I told Prof. Fernald that I was looking for living material of *Phryma Leptostachya* of North America, he at once kindly suggested that he would take me to the place where the plant was growing wild. On one Sunday morning, I dropped in Prof. Fernald's house, and drove my car to the suburbs with the Professor and his daughter on the back seat. He guided me nicely to the place, and I could successfully collect *Phryma*. Mainly based on this collection, I later revised the North American and Asiatic plants of the genus *Phryma*.

At the end of my stay I left a typewritten copy of a list of the plants common to Japan and North America in the hands of Prof. Fernald, and it is now preserved in the library of the Harvard Herbaria. I brought back to Japan some seeds of *Veroniscastrum virginicum* (L.) Farwell from the Gray botanic garden, and the plants raised from the seeds are still vigorously growing in my garden in Tokyo. They are not only one of my best memorial plants in the garden, but also they may possibly be the only living plant which has hitherto been continuously grown from the old Gray garden.

My knowledge of the North American plants obtained during my stay at Cambridge is really very useful for my further study on critical comparison between closely allied taxa of North America and Eastern Asia. These data were mostly arranged in order in my later papers such as 'Contributions to the study of variations in the Japanese plants closely related to those of Europe and North America' Part 1 and 2 (1952 & 56), and others.

In my memory, Prof. Fernald is still living as my dear father as well as my respected teacher. I will never forget his mild face, but with keen eyes.

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from Quentin Jones:

In the Fall of 1950, Professor Fernald was reading page proof of the 8th Edition. In fact, he was reading it to anyone that happened to cross the foyer of the old Gray Herbarium at the wrong time. Sometimes these "readings" lasted more than an hour. I was so favored on several occasions.

One occasion stands out in my memory because Professor Fernald got so much enjoyment out of the anecdote he told me. It seems that during his work on the Gaspé Peninsula he had a French-Canadian field assistant with the family name Assino, who kept needling Fernald to name a new species after him. Fernald never yielded to his pleading, "Because," he said, "can you see in print a specific epithet, *Assinoanus?*"

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from Alexander Lincoln, Jr.:

As a student in Professor Fernald's Botany 7 and Botany 10 courses in the early 1930's, I came to depend on my hurried walks up Garden Street to the Gray Herbarium of those days, set in the sunny Botanic Garden, as a very different atmosphere from the general drabness that tended to prevail elsewhere in Cambridge.

Botany 7 was handled in what, by contrast to the minutiae of microscopic peerings in other courses, achieved a grander scale: whole plants to be not only seen, but actually enjoyed; the tides of successive floras sweeping across the northern hemisphere, leaving scattered pockets of relict species and endemics; frequent allusion to local plant names and to plant uses of recent years if not still today, with particular emphasis on French Canada. Then, in Botany 10, opportunity to examine handsomely illustrated old volumes, themselves floras in a different sense, and to come to know more about early botanists and their travels, discoveries and conclusions.

Professor Fernald's classroom presence conveyed animation, deep interest and solid scholarship of the principles of systematic botany, along with sonorous, good-natured commentary from his wide range of field experience, all from a twinkley-eyed, somewhat rotund Santa Claus figure. His full gray beard, in colorful contrast with his often pink dome, underwent obvious change following a trim every couple of weeks or so. Originally opposed as I was to burdening our native plants with Latinized nomenclature, I came to enjoy the very sound of their names as pronounced by Professor Fernald, Professor Pease and others. Further, it soon grew apparent that Latin names provided a far superior method of distinguishing between species despite—over subsequent years—the annoyance of frequent name changes as dictated by botanical congresses.

It was always a pleasure to accompany Professor Fernald on a field trip, whether largely to collect plants or simply to learn more about them in their natural habitat. Especially on trips to Cape Cod, we were encouraged to taste them. Even in class, he sometimes brought in for our appraisal samples such as muffins he had made from acorns of white oak.

One mishap that occurred, as related to me later, interrupted the usual flow of an October outing. The professor, a non-swimmer, stepped off the end of a wall or low dam onto what appeared to be a leaf-strewn flat. But the leaves concealed instead deep water. He submerged to his chin before being helped out.

Professor Fernald remains a particularly helpful and influential star in the constellation of teachers I experienced at Harvard.

from Wayne E. Manning:

I first knew about Professor Fernald in the use of the 7th edition of *Gray's Manual*; Professor Wiegand at Cornell told us about him in taxonomy classes.

I first met Professor Fernald at the International Botanical Congress at Ithaca, NY in 1926. I recall that someone foolishly asked him whether he knew the name of a certain plant; of course he knew.

On the field trip in taxonomy the summer of 1926 I showed Professor Fernald the staminate flower buds of *Vallisneria spiralis*; he had never seen these. I had known them from collections of water plants for U.S. Biological Survey in Minnesota in 1923.

On a family trip through northern Maine in 1934, I collected a small-flowered waterlily and could not name it. On a trip to Harvard the following year I showed the specimen to Professor Fernald. He said that it was *Nymphaea tetragona*, not mentioned in the 8th edition of *Gray's Manual*. Then he said that he would tell me a story. He told me that Cyrus Pringle had collected a small-flowered waterlily in Maine in the 1870's, but the collection was lost. My collection was the first definite record for eastern U.S. Professor Fernald very kindly added a footnote to my report of the collection in the November 1936 issue of *Rhodora*.

My trips for research on the Juglandaceae in the library and herbarium at the Garden Street Gray Herbarium were limited in time, no more than 5 or 6 hours in any one day trip. It was a little bit exasperating to be asked by Professor Fernald to listen to his reading of his manuscripts, often critical comments about the publication of some botanical author. But of course it was pleasing to have a man of Professor Fernald's caliber to take notice of me, and I never left him until he was finished.

I knew that Professor Fernald was working on the 8th edition of *Gray's Manual*. On one of my trips to the Gray Herbarium in the late 1940's I asked Professor Fernald if I could see the manuscript of Juglandaceae. I realized at once that there were a large number of errors, but knowing his reaction to criticism by others, I said nothing. But that day I brought to him a number of specimens in "his" herbarium that meant that changes were necessary. Finally he asked me to take the copy of the mss. home to study and check over.

Of course that was just what I wanted, but now I had responsibility. I wrote out several pages of corrections of the mss., and finally dared to incorporate all of these in a corrected mss. to send to him. I was uncertain about his reaction. A short time later I received a postcard, saying: "I have spent a pleasant afternoon looking over the corrected mss. of the Juglandaceae you sent me. I am glad that someone understands the hickories." The material was published in the manual as I had written it and he kindly published a footnote in the manual that I had helped him with aid in the work on the family. My friends asked me how I had managed to have my name in *Gray's Manual.* I told them it was by hard work and good politics.

A short time later I sent Professor Fernald a mss. on the genus *Carya* for publishing in *Rhodora.* He realized that this involved changes for *Carya* in the manual I had not dared to incorporate these in the *Gray's Manual* mss. and he withheld publication of my material until after the publication of the manual.

I cherish very much my close connections with Professor Fernald.

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from Eugene Ogden:

I did graduate work with Professor Fernald 1934–1938. That was a very pleasant time for me, spending most of my time in the Gray Herbarium in the Harvard Botanical Garden.

I first met Prof. Fernald in July 1933 at meetings of the Josselyn Botanical Society at Winthrop, Maine where he invited me to continue botanical studies under his direction at Harvard and serve as Gray Herbarium photographer. During the four years there, he introduced me to many distinguished visiting botanists offering the Gray Herbarium photography services. During the fourth year it was my great privilege to be his laboratory assistant in plant taxonomy for Harvard and Radcliffe. In those days the Harvard boys and Radcliffe girls were in separate laboratories and on separate field trips. It was obvious that Prof. Fernald greatly enjoyed the two class trips to Cape Cod each October and the trips to Vermont each spring.

One of my fond memories is a brief trip with Prof. Fernald and his son, Henry, to the Catskill Mountains of New York in August 1935, presumably to look for nunataks, but I think Prof. Fernald had become a bit weary of herbarium work and needed some relaxation in the field. We found no nunataks. The car broke down, so we took rooms in an inn and that evening regaled each other with jokes. Prof. Fernald was partial to the pun type and supplied some clever ones. After the broken axle was replaced we made some collections, including a Gray Exsiccatae set of *Agrostis perennans*. On the way back to Cambridge we explored a small pond at Salisbury, Connecticut, for *Potamogeton longiligulatus*. I put on my swim trunks, but Prof. Fernald waded into the mucky water without removing coat and vest, the lower parts of which were submerged.

We didn't find the pondweed we were looking for. Prof. Fernald replaced his wet trousers with a dry pair, and we returned to Cambridge.

from Lilly M. Perry:

Dr. A. Lawrence Lowell once said, "What is there about the little flowers that makes the botanists quarrel with each other?" It was Professor Fernald who first mentioned to me that Dr. Robinson suggested before all his able students were placed, that they wanted a helper at the Gray Herbarium, and then he said if I were interested, to go see Dr. Robinson. Thus began my years at Harvard. As I was a special student of Professor E. C. Jeffrey, as soon as I returned from Fernald's taxonomic class, I have never forgotten Jeffrey's reply, "I have known Benjamin Robinson as a colleague for 23 years and I have never known him when he wasn't a gentleman, but be wary of the little man whose forehead reaches to the back of his neck." Before I took his class, former students had warned me to keep on his good side.

Professor Fernald was a brilliant writer, so much so that when he published narratives of his expeditions, many copies of these (so the librarian told me) were regularly bought by quite a number of people who had no particular interest in botany but valued them as good short story literature.

If you happened to drop in at the herbarium during the week, a familiar sight in our corner of the building would be Prof. Fernald reading a ms. to some person. Dr. Johnston used to say, "Don't be flattered, he's only polishing his ms. When I polish mine, I take it out the back door and read it aloud."

In all the years I put in at the Gray Herbarium, we clashed only once and then it was over a remark I thoughtlessly made. One Saturday afternoon I went to the herbarium to work on my research. Who should show up as I got nicely settled but M. L. F. He came over where I was and said, "Would you help me pack my trunk for Newfoundland?" So I went with him to the closet in the lab where both trunk and clothes were. Many times I had packed my own, always putting the delicate things in the top tray. I didn't even stop to think how he would pack his. After his personal things were tidily packed in the bottom he put in the tray. He had left his collecting materials for the tray. He had a pair of hip boots, vasculum, etc. I said where are you going to put your 7-league boots? Like a flash he said, "Don't be so personal," got up and left. I felt terrible, as I had always called those hip boots 7-league boots, but when I went to the main room he was gone. When I went to work Monday, the trunk was ready to ship.

Professor Fernald taught me the basis of herbarium work. (Dr. Robinson taught me how to use the library.) We started with Old World Juncus and Buchenov's work as Fernald was working on his Newfoundland collections and he wanted to see what was the relationship of the northern Old and New World species. He taught me how to compare literature and plants. You remember Jeffrey called him a little man. I was the shortest person on the staff and he was next. So many times when I worked with him, it happened that the plants he wanted to see (when we were working together) were in the top pigeonholes. I had to step up on the base (four inches) of the case, then hold on to the divider of the pigeonholes and reach up with my other hand for the covers in the top, he could just reach them comfortably; every time he asked me which one would get the plants up there, but always he got them. I put them away after he had seen what he wanted to know. One day I was working on the second balcony. Fernald came in with Rendle from the British Museum, who was spelling out for Fernald a scientific name ending in zia. The English *"zed"* Fernald didn't seem to understand, so I said in a very low voice "Zed is our *zee.*" Fernald turned at once and brought the specimen he wanted.

Fernald gave what we students called the Gossip Course. It was said that Asa Gray went abroad to study Botany, but his wife was interested in botanists. Anyhow, her results were in four big folios all wrapped in gray flannel covers and kept under lock and key.

They contained photographs of botanists and a full letter with salutation and signature (very important). Fernald chose from these the people he thought would be of value to us and told us what he thought would be of interest. I may say not all were Europeans. I remember two in particular: Britton, Director of the New York Botanical Garden, who was an able man; and Brandegee from California, although I understand he grew up in Brookline or its vicinity. I think he must have been a small man from what follows: One afternoon a large woman three or four steps ahead of a man came through the inner door and asked if this was the Gray Herbarium. On being told that it was, she turned around and said, "This is the place; come on, Dolly," to the man.

When Harvard had its 300th anniversary, he came into the library and said to me, "They only gave me one ticket for this afternoon. Shall I give it to you or Miss Stone?" I said, "Miss Stone, by all means. She's a regular staff member; I'm only here for the summer." I added it was probably only meant for a "Harvard man." His answer was, "You're as good a Harvard man as I know."

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from Hugh M. Raup:

My earliest impressions of Professor Fernald came while I was in graduate school in the mid-1920's and read some of his famous reviews. I did not know enough to understand and appreciate all the things he was writing about, but I do remember thinking that he really didn't need to be quite so vitriolic in his denunciations. These impressions made me rather timorous when I wrote to him in the spring of 1929 asking whether I would be welcomed if I came to study at the Gray Herbarium for a year beginning in the following autumn. I also inquired about some part-time assistantship that would help to pay expenses.

My wife and I had by that time accumulated a sizeable pile of specimens from three summers' plant collecting in northwestern Canada. By the fall of 1929 another summer's collections would be added to the pile. We realized that if we were ever to do anything with this material we would have to take it and ourselves to some large herbarium-library complex, preferably where there was someone with knowledge of the northern American flora. From all we could learn, Harvard would be the best place. I could use the Gray

Herbarium and my wife, who had collected the lichens, could use the Farlow. Hence my letter to Fernald.

To our amazement we had a reply almost by return mail, saying that I would indeed be welcomed, and that he would put me on as his assistant in his systematic botany course (Bot. 7). Naturally my misgivings about him began to evaporate at that point. When we arrived in Cambridge late in September he hadn't yet returned from Newfoundland where he had spent the summer. My first meeting with him was when he "bounced" into the Herbarium. I can think of no better word for the way he walked. He was about my height, but much larger in diameter. The top of his head was bald, but he had a full beard which was gray and I suppose could have been called a Vandyke, though it probably hadn't been trimmed since spring and had grown into a bush. His eyes were blue and twinkled at me over his half moon glasses. He quickly got me established with a place to work and storage space for the collections I had brought with me.

From then on he seemed to take a sort of fatherly interest in Lucy and me and our affairs. He was kindness itself. Very soon after we arrived he told us we should not expect to be entertained at his house because his wife was an invalid and they could not have guests. As we soon found out, however, this situation did not preclude his going out to dinner when invited. We availed ourselves of this proclivity on many occasions, usually when the monthly meetings of the Botanical Club came around. An old crony of Fernald's, J. F. Collins, would come up from Brown University and I would find both of them at the Herbarium and drive them to our house for a slightly early dinner, after which we would go downtown to the meeting. I suppose I should classify those occasions as "educational" for Lucy and me, which, of course, they were. We learned a lot from (and about) Fernald one of the main things we came to Cambridge to do. But over and above this, they were just unalloyed fun!

Both Collins and Fernald loved good food, and Fernald himself was not tyro as a cook. They regaled us with their experiences, usually hilarious, on their collecting trips to the Gaspé region. The conversation never flagged when they were there. Both of them were inveterate punsters.

Punning seemed to be epidemic around the Gray Herbarium in those days. I had lunch one day with Fernald and A. S. Pease at a small restaurant nearby. Soon after we had given our orders, one of them said something with a pun in it. This started a flood, and hardly a sentence was spoken between them throughout the meal that didn't have a pun in it. It was an exhibition of which I have often wished I had a record.

Fernald did many things for us that were beyond the call of duty. He piloted us on shopping expeditions to the push-cart markets at Faneuil Hall. They were held on Saturday nights, and he insisted that we should not get there until 9 o'clock when the prices would be coming down. We would meet him at Harvard Square and go on the subway, we with backpacks to carry home the plunder and he with a large, ancient and much battered suitcase. His procedure at the market was always the same. We first walked past all the carts, noting those that had the best stuff at the best prices. Then on the way back we bought what we wanted.

There was not much we could do for Fernald in return for all his kindness, but we did what we could. We had an automobile, such as it was—a Model T station wagon in which we had come to Cambridge. Fernald didn't drive and didn't own a car, so everywhere he went he walked, or used public transport, or got somebody to take him. For the last, of course, I offered my services, for which he was deeply appreciative. We used the car for class field trips and for miscellaneous other excursions, but he never overdid this, and was never demanding. One Sunday he asked if we would like to drive out to the wet meadows along the Concord River where he knew there were wild cranberries; we did, and came home with a few quarts of splendid fruit.

On another occasion in the first autumn we were here, he asked me to drive him down to Harwichport on the Cape. In the preceding spring, before he went off to Newfoundland, he had rented a cottage there in which his family would spend the summer. At the same time he put in a garden for them. They had tended the garden faithfully, harvested it in late summer, and had put up a huge amount of canned goods. Our trip was to bring it all to his house in Cambridge, which we did.

Except for one incident, I do not remember the details of that trip. We had started early in the morning so as to get back in one day. The weather was sunny, very cool and brilliantly clear, with a stiff westerly wind. In the latter part of the morning we were riding along a sandy road close beside a large cranberry bog surrounded by a wire fence. The preceding night had been frosty, and the bog had been flooded up nearly to the level of the road. The cranberries were ripening, and those that were already loose had floated to the surface of the water where the wind had blown them through the fence and piled them up right at the roadside. Fernald got me stopped and then hopped out with a basket. In no time he had scooped up at least half a bushel, and on we went. I was somewhat shocked by this procedure and asked him, rather circumspectly, whether it was legal. "Oh yes," he said, "any fruit found on the ground in a public right of way is public property, at least in Massachusetts."

At that time I was just beginning to learn something of Fernald's character. I found out a little later that what I had seen at the cranberry bog was thoroughly typical of Fernald. If we were riding along on some upland country road he would spot an orchard ahead, and, if it was immediately behind the bordering stonewall, with overhanding branches, we would stop and he would pick up a bag of apples. I had caught a glimpse of a phase of Fernald's character that could not even be guessed at from anything he ever published.

James Truslow Adams wrote in one of his pieces that the New Englanders had added an eleventh commandment to the Decalogue: "Thou shalt scrimp." Then there was the article I read in The New Yorker many years ago about an imaginary institution called the "N.E.S.P.D.I.P." which, being translated, was the "New England Society for the Prevention of Dipping into Principal." I once mentioned this to Helen Bailey (Mrs. Irving Bailey, for those who didn't know her), "Well," she said, "when I was a girl I was taught that I ought to live on the income from my income." The town dump for the village I live in is commonly spoken of as the "Petersham Exchange," which it really is.

I used to think that all such stories about these things were apocryphal. But after living in New England for over half a century I am convinced that they are founded upon solid fact. I can document this. I will even go so far as to suggest that New Englanders are already coded for scrimping and scrounging when they are born. My education along this line was begun by Fernald beside that cranberry bog.

Another opportunity for repaying Fernald for his kindness arose by pure chance. Student registration for courses occurred soon after we came. In those days there was no mixing of Radcliffe and Harvard students. Professor Fernald gave his Botany 7 lecture at 10 am to the Harvard boys, and at 11 am he did it all over again for the girls. That fall only two girls registered for the course, and there was an ironclad rule that a course could not be given for less than three. This precipitated a minor financial crisis! I say "minor", but it didn't seem so at the time. A substantial wedge of Fernald's salary came from that Radcliffe class, along with a much lesser though distinctly noticeable one in mine. When I told my wife about it that evening and she said "Why don't I register and take the class as a special student?" When I told Fernald this the next morning he all but fell on my neck. If Lucy had been there I think he would have kissed her. Shortly before Christmas he appeared at our door one Sunday morning with a little basket containing jars of assorted jams and jellies he had made from fruits he had gathered himself.

Our first child was born that year in mid-February. Term examinations were to be early in January, and Fernald was much concerned about how Lucy would get over to the Radcliffe campus from our apartment on Gibson Terrace if the day was stormy or icy. He went over to Radcliffe and arranged to have a proctor give her the examination at home if the weather was bad, but the day was bright, so she walked.

Fernald had a large, well furnished office on the second floor in the east wing of the Herbarium building, but I never saw him do any work there. He did his writing and studies of specimens and literature near one end of a long table that stood in the middle of the floor of the large rotunda-like room which was the central feature of the building. There he could see and be seen by anyone coming in the front door. I used to wonder why he thus made himself so readily accessible, but he seemed to prefer it that way.

His manuscript was all written by hand with a soft pencil on large sheets of cheap news-print paper, and was easily legible. He had a singular habit of reading it aloud, not to himself but to anyone who happened to come by and would listen. He always read with his pencil in his hand, using it to keep track of his lines, sentences, words and punctuation. If anything didn't sound quite right to him, he would stop and correct it, then go on. After I had been captured and read to a few times, it dawned on me that he wasn't doing it especially for my enlightenment. Rather, he was merely editing his own manuscript. Someone there listening might catch something that he missed.

Most of the people who came regularly to the Gray soon learned to avoid getting caught. If you could get through the front door very quickly and quietly, you could dodge around through various doors and passages and remain unseen until you got to where you needed to be. I did this too, on many occasions. But I must admit that I did a great deal of listening because I wanted to. Most of the things Fernald was writing about in the years when I was regularly or very frequently at the Gray were of immediate interest to me. I didn't need to read most of them when they were published because I had already heard their essentials.

Fernald's memory for the flowering plants and ferns of northeastern America was truly prodigious. The eighth edition of *Gray's Manual* listed over 8000 species and lesser categories, and I think it safe to say that he knew them all. His memory was not only for names, it extended to habitat and geographic data, and to a huge literature accumulated since the seventh edition was published in 1908. Most of this was scattered through miscellaneous journals and a few monographs, a great deal of it in *Rhodora,* but the only key to it was in Fernald's mind.

I was working on the flora of a part of N.W. Canada that was outside the ranges covered by any extant manual, but it was in the boreal forest where most of the species have wide east-west ranges, far enough east to be well within the *Gray's Manual* range, I would get stuck on a specimen, commonly a grass or sedge. I could get close to it in the Manual or the Herbarium but not close enough. I would show it to Fernald and he would immediately confirm or correct my diagnosis up to that point and admit that he couldn't go any further. Then he would get a far-away look in his eye and suggest that I look in the *Rhodora* volume for 1912. After this sort of thing had happened a dozen times or so it dawned on me that he had never been wrong!

Quite by chance, one day I saw an exhibition of his memory prowess. About 1938, Eric Hultén spent several months in this country and Canada visiting the larger herbaria and getting data for his great collection of spot maps of species ranges. He was several weeks at the Gray. He didn't think he would be likely to find much at the Arboretum herbarium but because he was here he might as well look. I told him I would take him over to Jamaica Plain and that he should stay at our house. I was to pick him up at the Gray in late afternoon. When I got there I couldn't find either him or

Fernald, even though I looked everywhere in the Herbarium. As a last resort I opened the door into Fernald's unused office, and there they were with their heads together over some specimens and maps, and surrounded by stacks of folders from the Herbarium. Hultén always carried with him a supply of blank maps, made at various scales. Fernald would turn over the sheets, glance at the labels, reach over with his trusty pencil, put the point down on the map, and Hultén would make another dot. If the specimen was one of his own collections, Fernald didn't even look at the label, for he would recognize the specimen itself and remember exactly where he had picked it up.

I don't know how long they had been at this, but Hultén's map for the Maritime Provinces, Newfoundland and southern Labrador was heavily sprinkled with dots. After I had watched for half an hour or so, they quit for the day and Hultén and I left. On the path out to the car, Hultén stopped in his tracks, turned to me and said, "Tell me—can Fernald really do this?" I said, "Well, I'm afraid he *can*." Then we went on to the car.

Anyone who reads what I have written about Fernald thus far would be thoroughly justified in considering that I became seriously biased by his unfailing cordiality and generosity to me and my family. I did, and still remain so. But as the years went on, the bias was severely tempered by events. I knew there was another side to his character, for I had seen it in those reviews I had read before I knew him. He had no patience with sloppy work or with good work that was poorly presented. Somehow, he contrived to take it as a personal insult when he was asked or required to read it. He could be just as irascible and thoughtless in his personal dealing with some people as he could be cordial and considerate with others. He would take instant and often firey dislikes to some people who came to him for advice or suggestions. There was no way to predict when this would happen.

Over the years I got the notion that Fernald really didn't like teaching. It took time away from his own studies, which he considered far more important. I never saw any evidence of preparation for his lectures in Botany 7. When our son was born in February of our first year in Cambridge, Lucy was out of the class for about six weeks, so I took notes for her. But the lectures, though always interesting (to me at least), were rambles in systematic botany. They could not be made to "parse."

He always had a few graduate students around, some of whom stayed with him through their doctorates while others migrated to other segments of Biology. He had a habit of giving a new student a taxonomic problem to cut his teeth on. This is a perfectly good idea, but it has to be used with consideration for the student's own preparation and proclivities. Also the problem has to be one that *can* be worked out in a relatively short time. Fernald seemed never to sense the need for all this. Rather, he would start a student off with a genus or section of a genus that was notoriously complex and difficult, such as *Poa* or *Calamagrostis* with which he himself had trouble. This led to early discouragement, and I think he lost some very good students by it. I suspect that one of the reasons he accepted me in the way he did was that I did not come to him as a student, thus relieving him of all the responsibilities for seeing me through course work, examinations, a thesis, and job hunting.

Fernald's flaring temper sometimes resulted in distinct disadvantage to his own work. One example of this is a case in which I had no part, but about which I had first hand reports. Fernald's famous paper on "Persistence of plants in unglaciated areas, etc.," published in 1925, invited serious criticism from the very beginning. Glacial geologists wrote it off immediately because they had no evidence that any of Fernald's unglaciated areas had actually escaped coverage by the Wisconsin ice. Another ready target was Fernald's use of negative evidence. A great many of his persisting plants had wide ranges in the northern Rocky Mountain region, while their representatives in the East were relatively rare and found only in small, restricted areas. Who was to say they were actually absent in the vast stretch of country between the lower St. Lawrence region and the Rockies? This question was particularly pointed because most of that country had never been seen by experienced botanical collectors. Still another serious question was biological, and involved the behavior of the plants themselves. If Fernald was correct in his persistence theory, the relict species were on hand and ready to move onto the newly exposed land when the ice melted away. But they had not done so, and were soon crowded into rarity by vigorous migrants from the south. Fernald had no good explanation for this, and could only propose that the plants were "senescent," "running down" as it were, as species were thought to do as they approached extinction.

Edgar Anderson was at the Arboretum for several years in the early 1930's where, among other things, he was making cytotaxonomic study of the genus *Iris*. He remembered that *Iris setosa* was one of Fernald's disjunct species having a wide range in the northern Rockies and Yukon, but with a single variety in small areas from southern Labrador to eastern Maine. He knew about the work of Turresson in Sweden and the ongoing transplant studies in California, both of them showing the significance of heritable ecotypic variation in species. He saw at once that here was a basis for explanation of the local behavior of disjunct species, and went over to the Gray to tell Fernald about it. Unfortunately it was the "wrong day," and Fernald exploded. He refused to have any part of it, and Andy was crushed. Why he took this line I do not know, but I have always considered the event as something of a tragedy. I think Fernald was being handed the first reasonable biological support his theory ever had, and he needed it.

I know of two cases in which Fernald apparently thought over his tirades and eventually "came around." In neither case did he ever say anything to me about how or why he did this.

The first was concerned with the publication of the Fernald and Kinsey book on "Edible wild plants, etc." I had learned about the manuscript of it soon after I came to Cambridge in 1929. Fernald had found out that I had, in previous years, made a lot of drawings of plants, and he got the notion that I could make illustrations for this manuscript which he hoped to get published "some day." One morning he came to my desk with it, sat down and started reading it to me. He spent most of the day at it! The book was of real interest to me but I couldn't get much excited about the drawings, for they would take a lot of time that I knew I wasn't going to have. Apparently Fernald got the message, and I heard no more about it for five or six years.

By that time I had moved my base of operations to the Arboretum and Dr. E. D. Merrill had become Director there. During his years at the New York Botanical Garden, Merrill had become well acquainted with Dr. E. G. Stillman who had long been a generous benefactor to Harvard. Dr. Stillman owned a large contract printing establishment in Cornwall, NY and carried around in his coat pocket the "office" of a tiny publishing business that he called the "Idlewild Press" and ran by himself. He was always on the lookout for odd manuscripts that were good but were not likely to be attractive to commercial houses. Merrill apparently told him about the Fernald-Kinsey manuscript at some time or other, and he immediately told Merrill to get hold of it and he would print it. Dr. Merrill talked it over with me and we debated at some length on how we would approach Fernald, which we would have to do first. Merrill was new here and had an idea that Fernald didn't like him very much, which I suspect was true. So the job fell to me and I tried it, with dismal and eruptive failure. Fernald absolutely refused to cooperate. This was my last personal involvement with "Edible wild plants." Two or three years later I heard by the grapevine that Fernald was getting the manuscript ready for printing, and in 1943 it was published by the Idlewild Press and printed at Dr. Stillman's Cornwall establishment. To this day I do not know how or why Fernald reversed himself so completely.

The second of these strange cases arose one morning when I found Fernald reading some galley proofs. He said he wanted to read me something, which turned out to be a review of Stanley Cain's book on "Foundations of plant geography", published in 1944. I had read the book and knew that it had some weak spots in it, but in spite of these I considered it to be by far the best thing available in the field it covered. Stanley had been at the Gray for two or three weeks while he was writing it, and I knew that Fernald liked him. But his review panned the book unmercifully. Fernald's specific complaints I could agree with, and did, for they dealt with floristic geography in which Stanley's treatment was not as up-to-date as it should have been. Otherwise I managed to say very little about the review, and promptly forgot it. A few weeks later a letter came from Stanley asking whether he should do anything about a letter he had just had from Fernald. In this letter Fernald told him he had written a review and had it in galleys, but after thinking it over had decided not to publish it. He had ordered the printer to break down the type. I told Stanley that I didn't know why Fernald had done this, but that I was pretty sure the letter was evidence of an entirely unique event and should be framed and hung in his office.

from Frank Seymour:

It is strange that I do not remember when I first met Dr. Merritt Lyndon Fernald. When I went to the Gray Herbarium to identify some specimens I had collected, I could not expect any attention from him. He was pointed out to me at a respectful distance: "That's Dr. Fernald."

For two or three summers before I entered Harvard I had been an herbarium assistant, so, I conferred with him frequently regarding my work. In my sophomore year (Sept. 1913–June 1914), I elected his famous course, Botany 7. With about 27 other students in an extraordinarily large class, we all enjoyed his humor. On reading what one member of the class had written in his examination paper, Dr. Fernald regaled all the members of the Staff with merriment over the exploits at what this student called "Gas Bay." One does not have to ponder long to guess in what field that student's father made his fortune.

The following year I was privileged to be Dr. Fernald's assistant in the same course, Botany 7. I listened with delight, the second time, to his lectures. A new feature that year was a lecture on famous botanists, especially American botanists.

The influence of the Continental Ice Sheets on the range of species, or, his account of that, made it extra interesting to me, about to begin my study of Marthas's Vineyard. Half of that island was covered by the Ice Sheet and the other half was not glaciated, at least, not by the most recent glacier. My study was carried on under the immediate direction of Dr. Fernald. It began with a series of collecting trips to the island. A few years later, accompanied by James M. Fogg, Dr. Fernald went to Martha's Vineyard for a brief collecting trip himself.

Dr. Fernald's greatness as a botanist is seen by comparing him with Linneaus. Linneaus entered the field when the science was comparatively new; he had the whole field before him. From it he could make multitudinous species. Fernald, in contrast, arose when New England had been hand-picked for new species by several generations of botanists. Yet new species kept popping up under his wonderful eyes and mind. If Linneaus had lived in Fernald's time, he might not have found as many species as Fernald.

Interrupted by my 18 months service in the U.S. Navy in World War I, I returned to work for Dr. Fernald only for about 4 months in 1919. After that my contacts with him were few as I moved out of easy reach of Harvard.

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from Lyman B. Smith:

Professor Fernald taught me to make superb herbarium specimens, to do bibliographic research, and to transfer personal enthusiasm into teaching.

First he learned from very fastidious amateurs to select not only the very best but to leave sufficient space for the label in the lower right corner and, if necessary, to choose smaller than average specimens with notes that they were selected small, and what size the plants in the stand would reach. A further refinement was extra flowers for dissection and Fernald's invention, the salivator, where a flower was held open by a bit of wet newssheet.

In drying, he at least experienced the full sweep of history from changing driers constantly with the necessity of drying the wet ones with luck by sunlight but more often by toasting before an open fire. Then came ventilators and circulating hot air which he at first rejected because ventilators used alone would often leave cross-bars on the specimens. Later he used driers between the ventilators and the specimen with good results. I do not remember his using metal ventilators but they have proved impractical because of weight and the tendency of local populations to appropriate them for roofing.

In the Gaspé in 1923, Fernald taught me to collect dwarf arctic types with my nose close to the ground; in the late 20's with his support, I began the collection of hundred sheet sets for the Plantae Exsiccatae Grayanae which was a graduate course in making good specimens and an introduction to bibliographic studies in making the manuscript for the printed labels. Each number had the significant references from one of Fernald's new species to others with a dozen references beginning with Linnaeus. Every reference had to be verified, which was not too difficult with the richness of the Gray Herbarium Library.

Fernald had little difficulty in transferring his enthusiasm for the taxonomy of the Gray's Manual Flora which he extended into Canada and Newfoundland because his students were already committed. However, he enlivened what could have been a dull memorizing of family characters by a wealth of anecdotes. He had his adventures and misadventures and frequently told ones on himself. One student enjoyed Botany 7 so much that he took a rerun by auditing it the next year and over 60 years later I still remember family characters by the stories with them. However, for the highest pitch of enthusiasm, one had to attend one of Fernald's lectures to the New England Botanical Club where he received almost revival meeting acclaim.

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from G. Ledyard Stebbins:

My association with Professor Fernald began when I took his course, Botany 7, in 1926–'27, continued until I left Harvard in the spring of 1931, and sporadically thereafter. Of the numerous memories I have of him, I select the following incident.

During my time the weekend field trips that he led in October to Cape Cod were exciting affairs that no botany student who was invited on them ever missed. Of the four that I attended, that of 1927 was the most memorable. On his Friday lecture, the day before we left, he said: "I've asked Harlow Bishop (one of Weston's graduate students) to help with transportation, so some of you will have to ride in his car, that he took to Gaspé last summer, and named 'Junkus canadensis' because of its erratic behavior. I've ridden in said car, and hope that it will hold up for the trip. However, I'm afraid that any time it could descend to the status of another species, 'Junkus inutilis.'"

These words were prophetic. The conversation came Saturday evening, just before dinner, in the main street of the town of Harwich. Fernald was as disturbed over the immobile vehicle as we were, and gallantly joined the push-crew that was removing it from the center of the street to an acceptable parking place. In doing so, he failed to realize the modest speed that it would acquire with everybody pushing it. All of a sudden, we found him on the pavement, with his foot pinioned down by the front wheel. We quickly extricated him, and carried him to the restaurant for dinner and to his lodging. Meanwhile, Bishop was able to get the car going, at least temporarily.

We all expected that this disaster would end our trip. Not so, said Professor Fernald. His foot had been examined and the damage was minor. So the next day we drove over the usual tour of dunes and sandy pond margins filled with the rare species that he knew and loved so well. At every stop, two stout and faithful students would make with their arms a comfortable sedan chair and carry him to the pond margin, while other students brought him the specimens to which he pointed. He would then give his inimitable descriptions of the geographic distribution, relationships and other valuable information about each species that he knew so well. The performance appeared like a miniature version of Sir Joseph Hooker in India, making notable botanical pronouncements from the howdah on the back of an elephant. We were even more impressed than we would have been without the accident.

HOLOCENE FRUIT, SEED AND LEAF FLORA FROM RIVERINE SEDIMENTS NEAR NEW HAVEN, CONNECTICUT

LEE S. PIERCE AND BRUCE H. TIFFNEY

ABSTRACT

Fruits, seeds and leaves of 48 gymnosperm and angiosperm taxa are reported from 2830±70 and 2680±30 year-old riverine sediments located just north of New Haven, Connecticut. Most of the fossils are identified to species, providing refinement of previously available pollen data; several species are not commonly found in Holocene pollen floras.

Key Words: Holocene flora, riverine sediments, central Connecticut

INTRODUCTION

The post-glacial history of the flora and vegetation of the eastern United States has been reconstructed from studies of fossil pollen, and less commonly from fruits, seeds and leaves (Davis, 1969a, 1976; Bernabo and Webb, 1977; Delcourt and Delcourt, 1981; Webb, 1981). We present data on a macrofossil flora collected from riverine sands that were deposited about 2700 years before present (YBP) just north of New Haven, Connecticut. We describe the sediments and give a brief paleoecological interpretation of these data.

The New Haven flora is significant for two reasons: it is a macrofossil flora and it was collected from a river valley in Connecticut's central lowland. Macrofossils, in contrast to pollen, are generally derived only from plants living near the site of deposition (McQueen, 1969; Birks, 1973; Spicer, 1981) and are frequently identifiable to the species level, thus providing local ecological details which studies of pollen cannot supply. Qualitative information from macrofossils complements quantitative information derived from pollen (Watts and Winter, 1966), the source flora and deposition of which can be statistically characterized (e.g. Davis and Webb, 1975; Webb and McAndrews, 1976; Webb et al., 1978; Webb et al., 1981). Modern studies of Holocene macrofossils emphasize collection techniques that permit a similar quantitative reconstruction of the source vegetation (Watts, 1979; Baker et al. ,1980; Davis et al., 1980, Delcourt et al., 1980; Barnosky, 1981). Unfortunately, much of the material available for the present study was collected at an earlier time, and cannot be replicated; hence we limit our contribution to a description of the flora.

The importance of a lowland river deposit is unique in that most sites studied in New England have been upland lakes (D. Gaudreau, pers. comm.), including the best studied site in Connecticut, Roger's Lake (Davis, 1969b and references therein). Traditionally, Quaternary palynologists have not studied river deposits because such pollen floras are the product not only of the source vegetation and wind patterns, but also of the sorting of pollen grains by flowing water. This last taphonomic variable, which affects macrofossil floras to a lesser degree, cannot be easily characterized. Thus, this flora presents data on a rarely sampled community.

SITE DESCRIPTION

The fossils were collected on the property of Landfill Associates Inc., formerly the Stiles Clay Pit, on the west margin of the Quinnipiac River (41°21′49″N, 72°53′7″W) in Hamden, Connecticut. Clay mining ceased at this site several years ago; it is presently a sanitary landfill. Excavations for sand and clay to cover refuse have exposed a face that is approximately 5 meters high and about 100 meters long. This section (Figure 1) reveals a series of clays, sands and peats (Bloom, 1968).

The bottom of the exposed face rests on the red clays of the New Haven formation, deposited in a glacial lake approximately 12,000 YBP (Brown, 1930). The clay is reported to contain fossils of tundra plants (Beinecke and Siccama, 1973,), but no published evidence exists, and we were unable to locate any such fossils in the field.

The clay is disconformably overlain by 2.6 to 2.9 meters of cross-bedded, quartz-rich sands deposited by the Quinnipiac River following draining of the glacial lake. This unit is gravel at the contact with the clay, but grades rapidly into sand which becomes increasingly fine toward the top of the unit. The basal portions contain many transported logs of *Quercus* L. (two species), *Tsuga* (L.) Carr. and *Acer* L. (Brown, 1930) together with smaller plant fragments. These remains have been radiocarbon dated at 6810±170 YBP (Stuiver and Deevey, 1961). The upper portions of the sandy unit contain frequent lenses of leaves, fruits and seeds. Wood from this part of the unit has been dated at 3560±180 YBP (Stuiver et al., 1963),

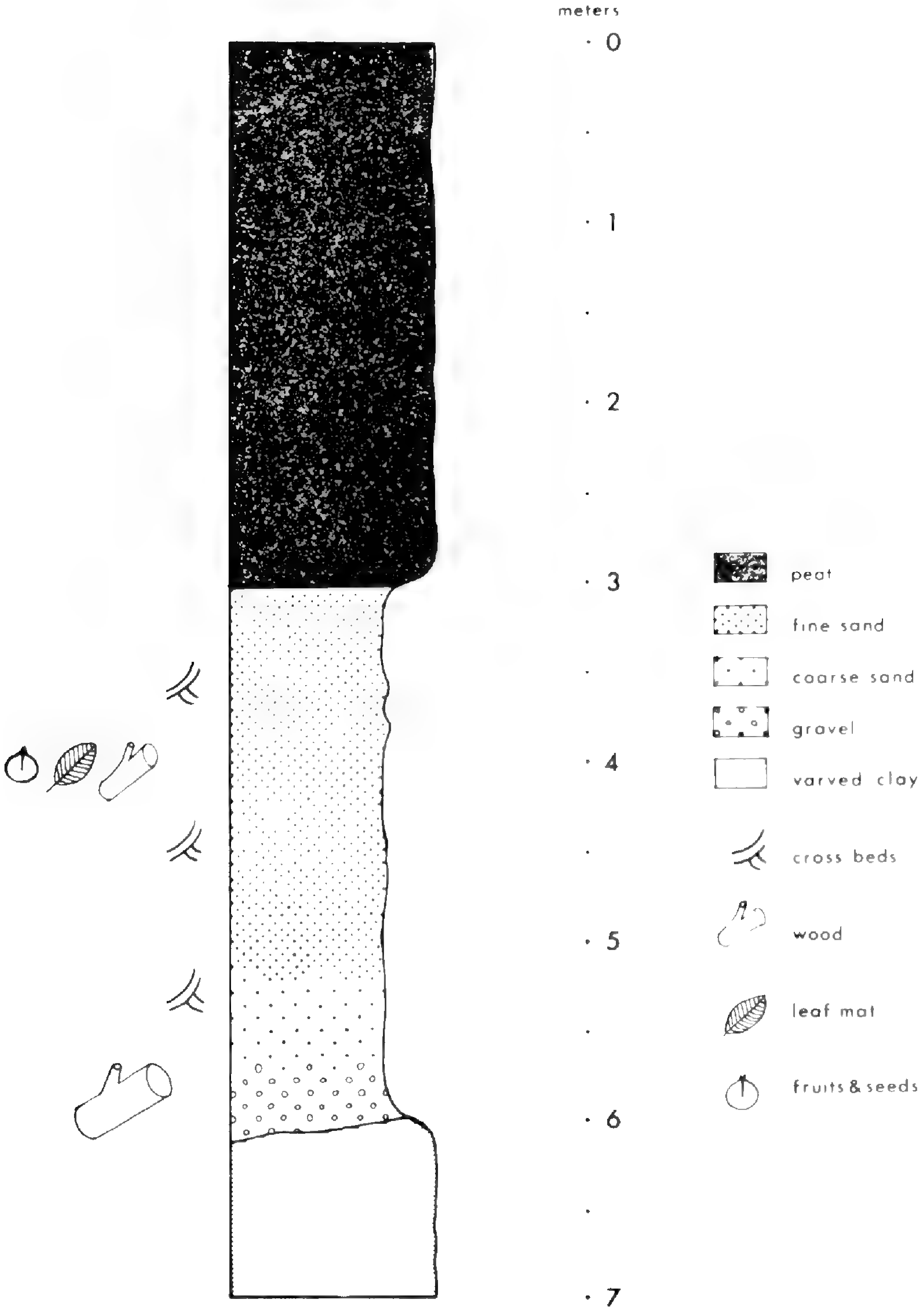


Figure 1. Stratigraphic section, west margin, Quinnipiac River, Hamden, Conn. Data from Brown, 1930, Siccama (Personal data, unpublished) and field observations by the authors.

hickory nuts at 2830±70 and butternuts at 2680±30 YBP (Quaternary Isotype Laboratory, University of Washington, Seattle; November, 1984; specimens QL-1881 and QL-1882).

The crossbedded sands are topped by 1.7 meters of *Spartina* peat and 0.3 meters of *Typha* peat. The *Spartina* peat correlates with other evidence (Sears, 1963; Bloom and Stuiver, 1963) for rising sea levels in the last 7000 years. As the sea level rose, the boundary between salt water and flowing fresh water retreated up the Quinnipiac River. The arrival of this interface at the fossil locality is marked by truncation of the riverine sands by *Spartina* salt marsh peat. Human interference in the early 1900's restricted tidal flow in the lower Quinnipiac, and consequently the fresh water *Typha* marsh now occupying the site became established (Beinecke and Siccama, 1973).

MATERIALS AND METHODS

Lenses of fruits, seeds and wood and leaf mats were collected from the upper half of the gravel-sand unit. Specimens from the two richest lenses of fruits and seeds were radiocarbon dated at 2870±70 YBP (specimens of *Carya cordiformis* (Wang) K. Koch) and 2680±30 YBP (specimens of *Juglans cinerea* L.). (Quaternary Isotype Laboratory, University of Washington, Seattle; November, 1984; specimens QL-1881 and QL-1882). The species present in these collections are listed in Table 1.

Fruits and seeds were identified by comparison to descriptions, photographs and drawings in Ogden (1953), Brouwer and Stahlin (1955), Martin and Barkley (1961), Katz et al. (1965), Berggren (1969), Seymour (1969), Fernald (1970), Schopmeyer (1974), Montgomery (1977), Elias (1980), and Hellquist and Crow (1980), and by comparison to specimens in YU, A and GH. Leaves were identified similarly from Petrides (1958), Symonds (1958, 1963), Fernald (1970), and Elias (1980), and by comparison with YU, A and GH specimens.

Photos of small fruits and seeds were taken on Kodak Panatomic Film with a Nikon PMF photo attachment mounted on a Nikon SMZ-10 binocular dissecting microscope. Photos of leaves and large nuts were taken with a 35 mm camera with a 55 mm macrolens.

SYSTEMATICS

The nomenclature used here is that of Fernald (1970). The descriptions of leaf venation follow the method of Hickey (1973). Fruits and seeds with bilateral symmetry are described by naming the plane figures which would be seen if they were sectioned along the plane of symmetry (sagittal section), along a plane that is perpendicular to the plane of symmetry and which includes the longest axis of the plane of symmetry (frontal section), and along a plane perpendicular to the two previously described planes (transverse section). When "base" and "apex" are used to describe fruits, they refer to the pedicellate or pedunculate and stigmatic ends, respectively. For seeds, the chalaza occurs at the base, the micropyle at the apex. The fruit and seed specimens cited in this study are stored in the Paleobotanical Collections of the Peabody Museum, Yale University, collection numbers 4649 through 4825. Figured leaf specimens, which were difficult to preserve, were not saved; leaf-bearing bulk samples are also available in the Paleobotanical Collections.

LIST OF SPECIES

PINACEAE

Abies balsamea (L.) Mill.: Rare.

The 4-mm-long seed is oblong in sagittal section, lenticular in transverse section and elliptic in frontal section, is angled on one margin and has concave sides along the other margin, a common feature in *Abies* seeds. Figure 2.

Pinus L. or **Picea** Dietr. sp.: Rare.

The 4-mm-long, oblong, lenticular, elliptic (sagit., trans. and frontal sections, respectively) seed is *Pinus* or *Picea,* but without the presence of a wing, it is impossible to determine which it is. Figure 3.

Tsuga canadensis (L.) Carr.: Several.

The ellipsoid cones are 1.2 to 1.9 cm long, with scales that are almost as long as they are broad. Figure 4.

SPARGANIACEAE

Sparganium eurycarpum Engelm.: Several.

The 6 to 8 mm broad pithy shoulders of the 8 to 10 mm long

Table 1. Species identified from two dated samples, and three associated but undated samples, of fruits, seeds and leaves collected in Holocene sediments near New Haven, Connecticut.

	2830±70	2680±30	Undated		
	YBP	YBP	Lens 1.	Lens 2.	Leaf Mat
PINACEAE					
Abies balsamea		+			
Pinus or *Picea* sp.		+			
Tsuga canadensis	+	+			
SPARGANIACEAE					
Sparganium eurycarpum	+	+	+		
Sparganium cf. *americanum*	+	+			
Sparganium cf. *fluctuans*	+	+			
ZOSTERACEAE					
Potamogeton nodosus	+	+	+	+	
Potamogeton pulcher	+				
Potamogeton vaginatus	+	+			
Ruppia maritima	+				
Zannichellia palustris	+	+		+	
CYPERACEAE					
Carex lupulina	+	+	+		
Cladium mariscoides	+	+	+		
Dulichium arundinaceum	+	+			
Scirpus, two species	+	+	+	+	
LILIACEAE					
Smilax sp.					+
MYRICACEAE					
Myrica pensylvanica	+				
JUGLANDACEAE					
Carya cordiformis	+				
Carya ovata	+	+	+		
Juglans cinerea	+	+	+		
CORYLACEAE					
Carpinus caroliniana		+			
Ostrya virginiana	+	+			
Alnus sp.	+	+			
FAGACEAE					
Fagus grandifolia	+	+	+	+	+
Quercus alba	+				+
Quercus coccinea	+				?
POLYGONACEAE					
Polygonum, three species	+	+	+	(2)	

CERATOPHYLLACEAE					
Ceratophyllum echinatum		+			
NYMPHACEAE					
Brasenia schreberi	+				
RANUNCULACEAE					
Ranunculus cf. *trichophyllus*	+	+	+		
MAGNOLIACEAE					
Liriodendron tulipfera	+	+	+		
PLATANACEAE					
Platanus occidentalis	+	+	+		+
ROSACEAE					
Prunus nigra	+				
Rubus sp.	+		+		
Crataegus sp.	+	+			
STAPHYLEACEAE					
Staphylea trifolia	+	+	+		
ACERACEAE					
Acer sp.		+			
Acer saccharum					+
VITACEAE					
Parthenocissus sp.	+	+	+		
Vitis labrusca	+	+	+		
TILIACEAE					
Tilia americana		+	+	+	+
VIOLACEAE					
Viola sp.		+			
NYSSACEAE					
Nyssa sylvatica	+	+			
CORNACEAE					
Cornus alternifolia	+				
Cornus ammomum	+	+			
Cornus drummondi	+	+			
ERICACEAE					
Genus indet.	+	+	+	+	
CAPRIFOLIACEAE					
Sambucus canadensis	+	+	+	+	
Sambucus pubens	+		+		
COMPOSITAE					
Ambrosia artemisiifolia	+	+	+	+	
Ambrosia trifida	+	+			
Helianthus cf. *decapetalus*	+				

obtriangular achene are characteristic of this species. Several specimens have two seed chambers. Figure 5.

Sparganium cf. **americanum** Nutt.: Rare.

The narrow obovoid achene is 5.8 mm long, 2.1 mm in diameter, with a blunt apex and a narrowed base. This description agrees with *S. americanum,* but the achene is also similar to the slightly larger fruits of *S. androcladum* (Engelm.) Morong. Figure 6.

Sparganium cf. **fluctuans** (Morong) Robbins.: Rare.

The obovoid achene is 4.5 mm long, 2.1 mm in diameter, has an enlarged, blunt apex tipped with a broken falcate stigma and a narrow and elongate base. Although similar to *S. angustifolium* Michx. and *S. multipedunculatum* (Morong) Rydb., the fossils lack the constriction common in fruits of these two species. Figure 7.

ZOSTERACEAE

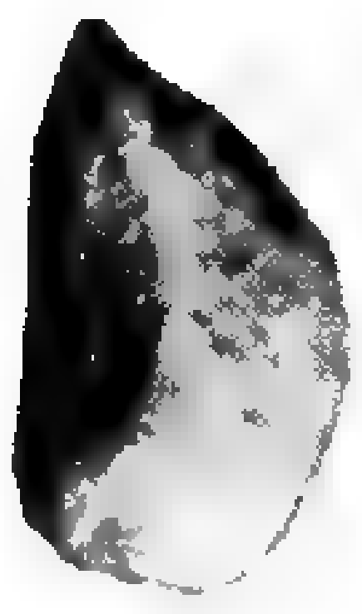
Potamogeton nodosus Poiret: Several.

The 4-mm-long endocarp is broadly elliptic in sagittal section, narrowly elliptic in transverse section, oblong in frontal section, has an undulating keel along the valve, an apical style base near the margin opposite the valve, and convex sides. Figure 8.

Potamogeton pulcher Tuckerman. Several.

The 3.8-mm-long endocarp is obliquely obovate in sagittal section, oblong in transverse and frontal sections, has a rounded keel on the valve, a central projection on the opposite margin and three basal projections. Figure 9.

Figures 2–25. Specimen identifications as indicated; further discussion in the text. **2.** *Abies balsamea.* Seed without wing. ×4. **3.** *Pinus* sp. or *Picea* sp. Seed without wing. ×4. **4.** *Tsuga canadensis.* Ovulate strobilus. ×1.5. **5.** *Sparganium eurycarpum.* Achene. ×4. **6.** *Sparganium* cf. *americanum.* Achene. ×4. **7.** *Sparganium* cf. *fluctuans.* Achene. ×5. **8.** *Potamogeton nodosus.* Endocarp. ×4. **9.** *Potamogeton pulcher.* Endocarp. ×4. **10.** *Potamogeton vaginatus.* Endocarp. ×4. **11.** *Ruppia maritima.* Achene. ×6. **12.** *Zannichellia palustris.* Achene. ×6. **13.** *Carex* cf. *lupulina.* Achene. ×3. **14.** *Dulichium arundinaceum.* Achene. ×4. **15.** *Cladium mariscoides.* Achene. ×5. **16.** *Scirpus* species one. Achene. ×5. **17.** *Scirpus* species two. Achene. ×5. **18.** *Myrica pensylvanica.* Endocarp. ×5. **19.** Carya ovata. Nut. ×1.3. **20.** *Carya cordiformis.* Nut. ×1.3. **21.** *Juglans cinerea.* Nut. ×0.75. **22.** *Alnus* sp. Ovulate catkin. ×2. **23.** *Alnus* sp. Scale of ovulate catkin. ×6.3. **24.** *Ostrya virginiana.* Nut. ×4. **25.** *Carpinus caroliniana.* Nut. ×4.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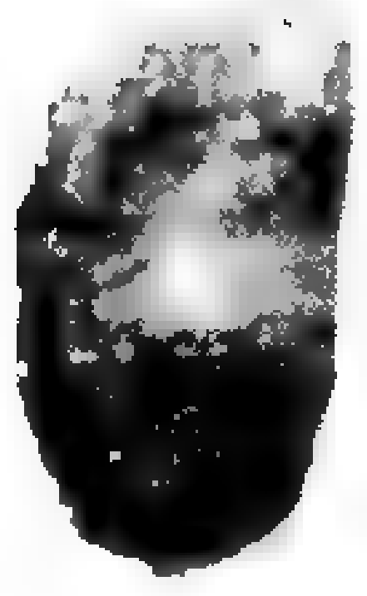
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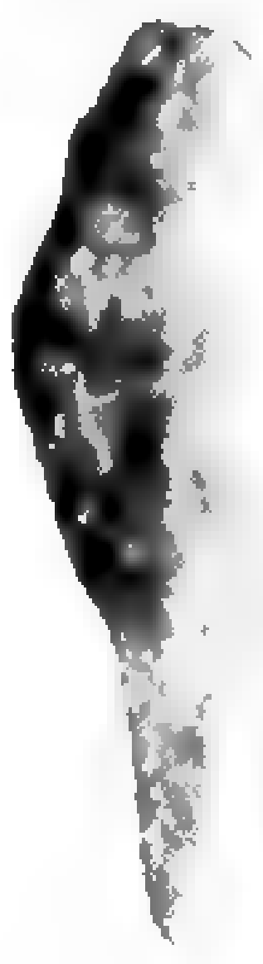
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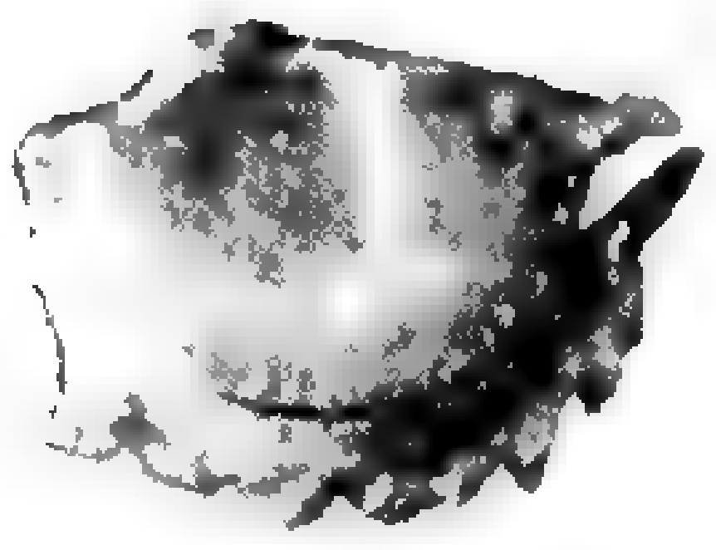
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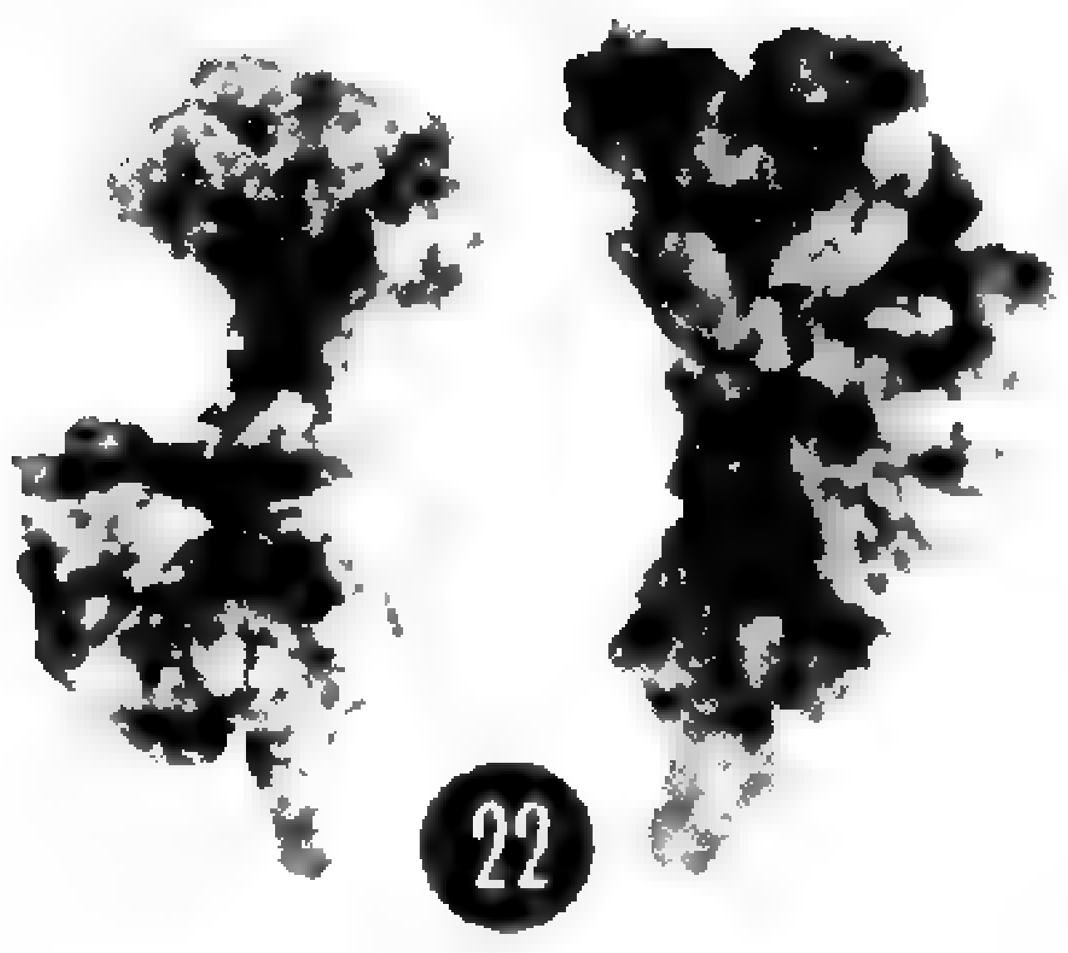
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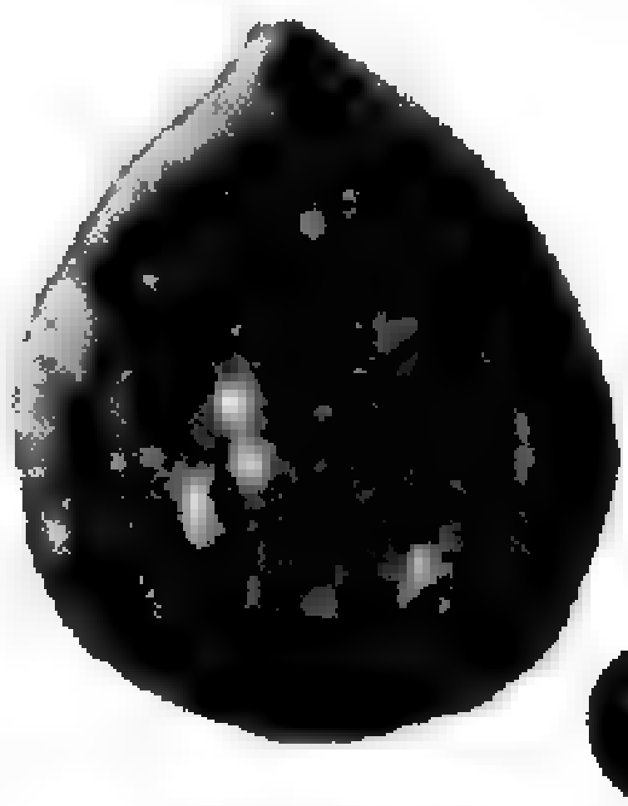
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Potamogeton vaginatus Turczaniow. Several.

The 3.3-mm-long endocarp is roughly broad elliptic in sagittal section with a sinusoidal dorsal margin, is ovate in transverse and frontal section, has concave sides and no keels or projections. Figure 10.

Ruppia maritima L.: Rare.

The less-than-2 mm-long, compressed ellipsoid achene has a persistent style similar to that of *Potamogeton,* but which extends beyond the body of the seed to form an apical beak. Figure 11.

Zannichellia palustris L.: Rare.

The 2.5 mm-long, flattish achene is oblong-arched in sagitittal section, has a stalk at one end, a style base at the other, and spine-like projections along both sides. Figure 12.

CYPERACEAE

Carex lupulina Muhl.: Several.

The achenes average 3.7 × 2.3 × 2.3 mm and are elliptic in frontal section, triangular in transverse section, with a long or contorted style and a stipitate base. Figure 13.

Dulichium arundiaceum (L.) Britt.: Rare.

The flattish oblong achene plus style averages 5 mm in length and possesses six to nine basally-attached bristles which are longer than the achene and style together. Figure 14.

Cladium mariscoides (Muhl.) Torr.: Rare.

The achene is 2 mm in diameter. The soft outer covering has been eroded, revealing a sphere with three longitudinal ridges and a distinctive basal ring. Figure 15.

Scirpus species one: Numerous.

The achene is 2.5 mm long, 1.5 mm wide, obovate to plano-convex (sagit.), elliptic to plano-convex (trans.), obovate (front.), with a few attached bristles. It is similar to *S. acutus* Muhl. or *S. validus* Vahl. Figure 16.

Scirpus species two: Numerous.

The achene is 3.2 mm long, 2.9 mm wide, plano-convex (sagit., trans.), obovate (front.). It is similar to *S. fluviatilis* (Torr.) Gray and *S. robustus* Pursh. Figure 17.

LILIACEAE

Smilax L. sp.: Rare.

The obovate leaf with a cordate base has basal perfect acrodromous venation. The specimen is too poor to permit species determination. Figure 58.

MYRICACEAE

Myrica pensylvanica Loisel.: Rare.

A 3 × 2.5 mm ovoid endocarp with thick walls which thin at the apex. Seeds of *M. gale* L. are narrowly ellipsoid. Figure 18.

JUGLANDACEAE

Carya ovata (Mill) K. Koch.: Several.

The ellipsoid nut is 2 cm in diameter, four-angled in transverse section with a smooth surface. Figure 19.

Carya cordiformis (Wang) K. Koch.: Rare.

The subglobose nut is 2 cm in diameter, with an apical mucro and a faintly ridged but otherwise smooth surface. *C. glabra* has a more clearly ridged and nerved surface. Figure 20.

Juglans cinerea L.: Several.

The elongate-ellipsoid nut is 4 × 2.5 cm with a round base, pointed apex, and strong, ragged, longitudinal ribs. Figure 21.

CORYLACEAE

Alnus Mill. sp.: Several.

The catkin is composed of many scales which are thickest at their apices. A species determination is not possible. Figures 22, 23.

Ostrya virginiana (Mill.) K. Koch: Rare.

The 5.5 mm-long × 3 mm in diameter nut is compressed-lanceoloid to ovoid, with a smooth to faintly striate surface. Figure 24.

Carpinus caroliniana Walt.: Several.

The nut is 2.7 × 2.4 × 1.2 mm, compressed-ovoid with three or four prominent ridges on both faces, and ridges along the margins. Figure 25.

FAGACEAE

Fagus grandifolia Ehrh.: Numerous.

The nut is obovate in frontal section, 10 to 15 mm long and 5 to 10 mm wide, has a distinct triangular transverse section, and is borne in an involucre with four elliptic, tuberculate valves. The elliptic leaf has a short to long acute apex, acute base, pinnate primary venation, craspedodromous secondary venation and toothed margins with one tooth per secondary vein. Figures 26–28, 59.

Quercus alba L.: Rare.

The involucre is 8 mm deep and 12 mm wide, covered by rounded tuberculate scales which are not joined at the base of the cupule. This suite of characters fits only *Q. alba* of the *Quercus* species in the northeastern United States. The leaf, which has pinnate primary venation and craspedodromous secondary venation, is obovate and has obliquely descending sinuses; the four pairs of ascending lobes are narrowly oblong and are not tipped with bristles. These features also conform to *Q. alba.* Comparisons could be made to *Q. stellata* Wang. or *Q. macrocarpa* Michx., but these do not match in all characters. Figures 29, 60.

Quercus coccinea Meunch.: Rare.

The 5 mm-deep and 8 mm-wide involucre is closely covered by tapering truncate scales. These cupules are clearly those of *Q. coccinea* Meunch. Associated leaves with deep sinuses and bristle-tipped lobes and pinnate craspedodromous veins agree with those of *Q. coccinea,* but could possibly represent another species. Figures 30, 61.

Figures 26–42. Specimen identifications as indicated; further discussion in the text. **26.** *Fagus grandifolia.* Involucre. ×1.5. **27.** *Fagus grandifolia.* Scale of involucre. ×1.7. **28.** *Fagus grandifolia.* Nut. ×1.7. **29.** *Quercus alba.* One half of involucre, three views. ×2. **30.** *Quercus coccinea.* Involucre, three views. ×2.3. **31.** *Polygonum* species one. Achene. ×5. **32.** *Polygonum* species two. Achene. ×4. **33.** *Polygonum* species three. Achene ×7.5. **34.** *Ceratophyllum echinatum.* Nutlet. ×4. **35.** *Brasenia schreberi.* Seed. ×4. **36.** *Ranunculus* cf. *trichophyllus.* Achene. ×5. **37.** *Liriodendron tulipifera.* Seed. ×4. **38.** *Platanus occidentalis.* Receptacle. ×2. **39.** *Rubus* sp. Pyrene. ×4. **40.** *Crateagus* sp. Nutlet. ×4. **41.** *Prunus nigra.* Endocarp. ×2. **42.** *Staphylea trifolia.* Seed. ×4.


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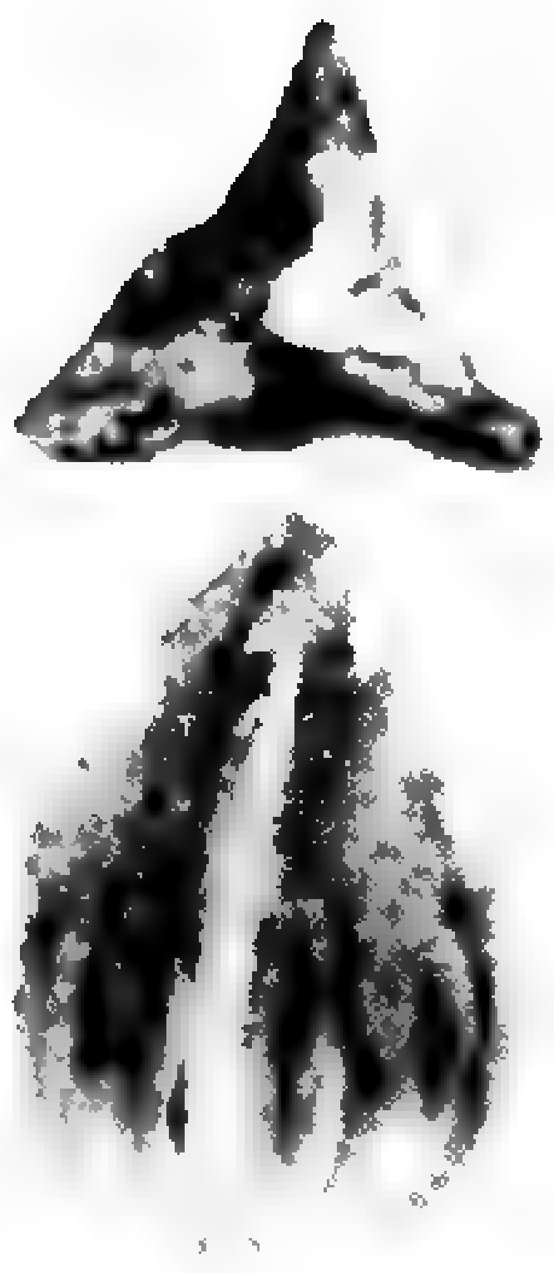


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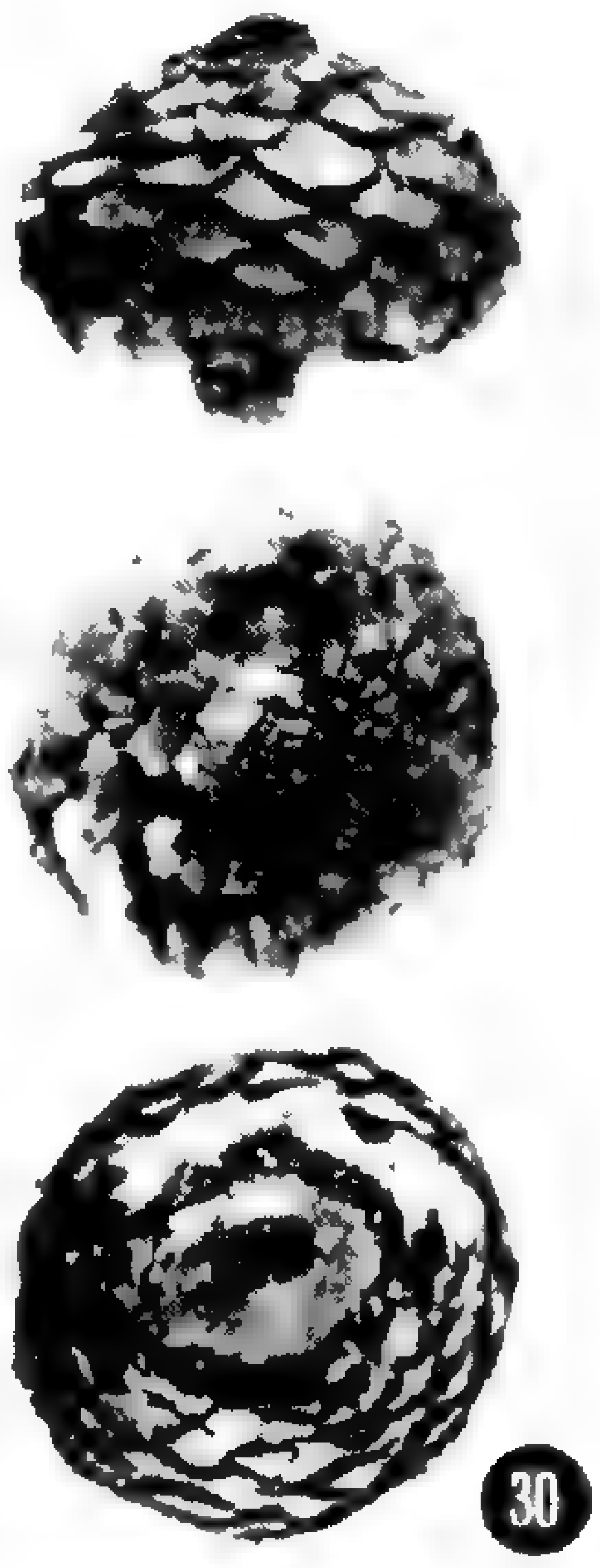
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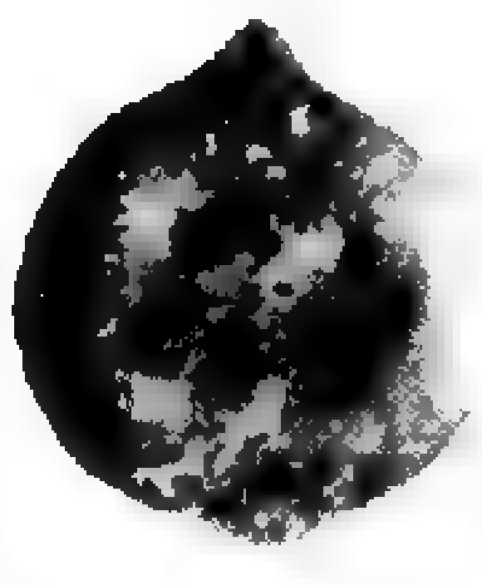
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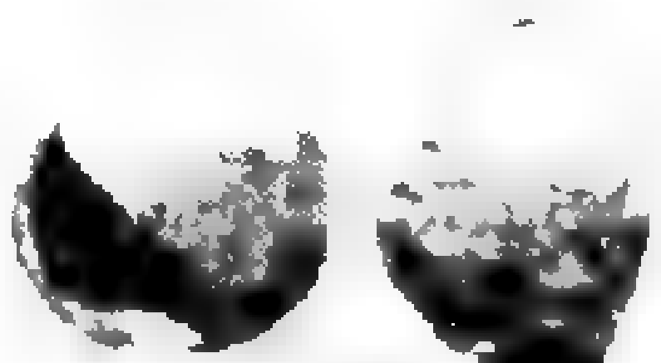
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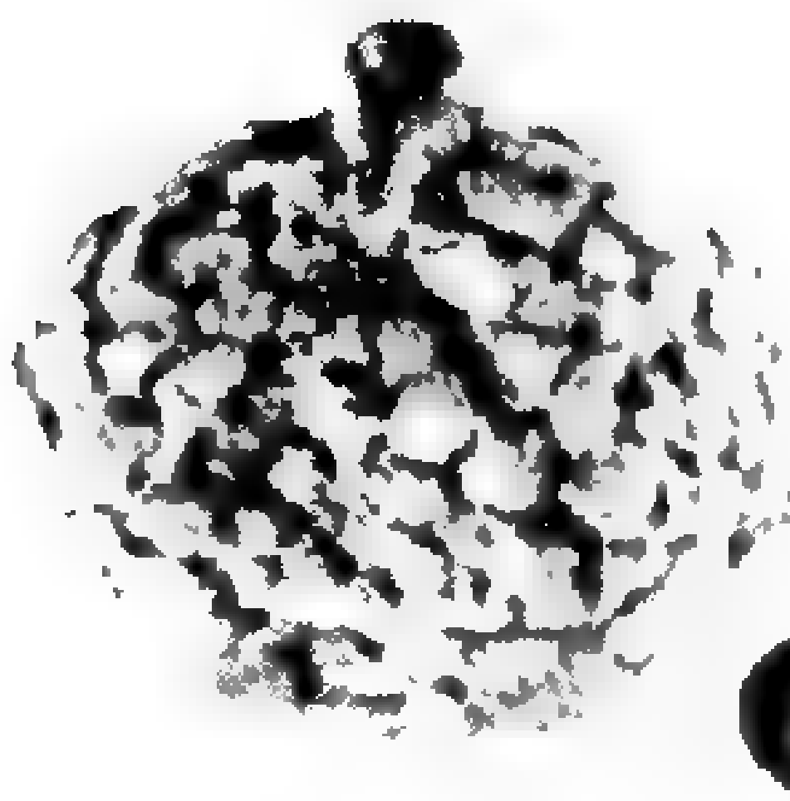
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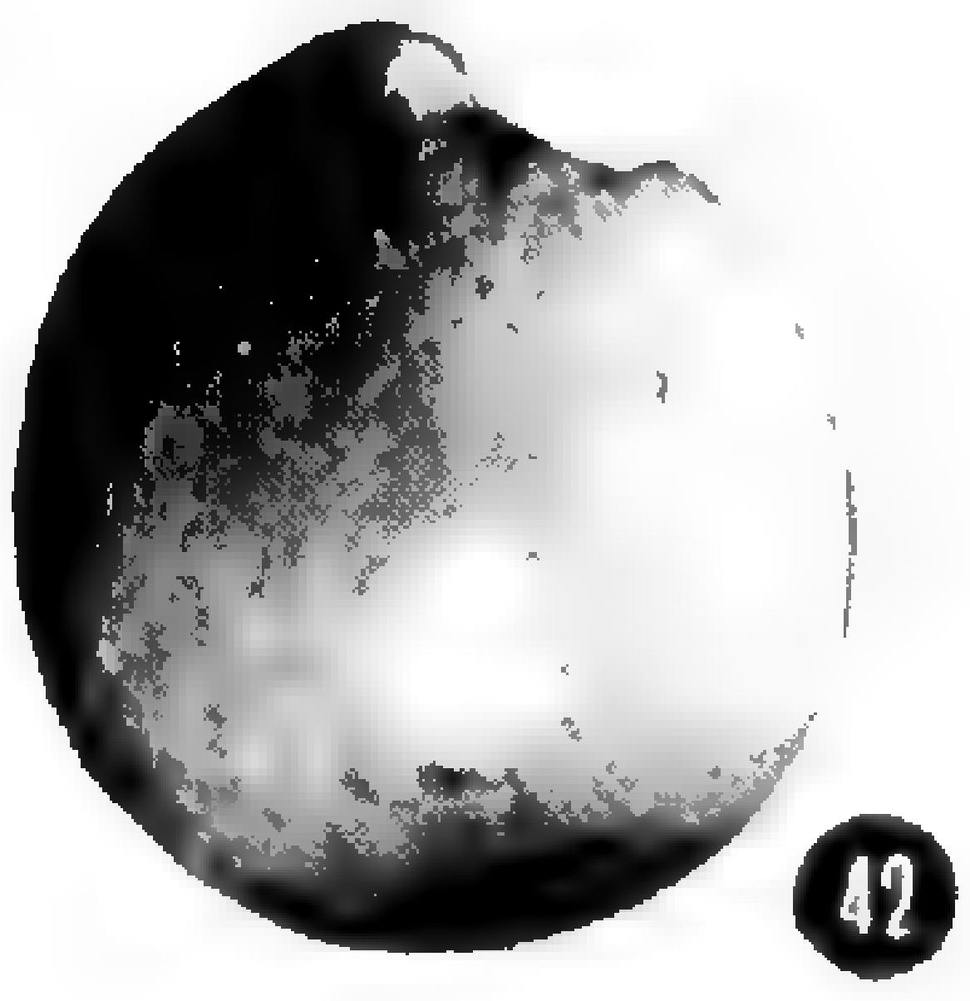
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POLYGONACEAE

Polygonum L. species one: Several.

The achene is 4.3 mm long × 2.5 mm wide, elliptic (front), sharply three-angled with concave faces, yielding a star-like transverse section. Similar achenes with concave faces are seen in *P. douglasii* Greene and *P. sagitittatum* L., among other species. Figure 31.

Polygonum L. species two: Several.

The achene is 4.6 mm long × 2.5 mm in diameter, is triangular in transverse section and elliptic in frontal section. The fossils are similar to the achenes of *P. robustius* (Small) Fern., but this is a common achene shape. Figure 32.

Polygonum L. species three: Rare.

The achene is 2 mm long × 1.8 mm wide, compressed-ovoid, with a small apical projection. The shape and small size are similar to *P. lapathifolium* L., but this is a common achene shape among species of *Polygonum*. Figure 33.

CERATOPHYLLACEAE

Ceratophyllum echinatum Gray.: Rare.

The 6 mm-long nutlet is lenticular in sagittal and transverse sections, elliptic in frontal section, has three marginal spines plus the bases of others which have been broken off. The number of spines, plus the narrow marginal wing produced by their bases, indicate that this is *C. echinatum* and not *C. demersum* L. Figure 34.

NYMPHAEACEAE

Brasenia schreberi Gmel.: Rare.

The 2.5 × 2 mm ellipsoid seed has a tuberculate surface and a basal attachment scar. Figure 35.

RANUNCULACEAE

Ranunculus cf. **trichophyllus** Chaix.: Rare.

The 2 mm-long compressed ellipsoid achene is rugose, lacks a stylar beak and is not sharply keeled. Figure 36.

MAGNOLIACEAE

Liriodendron tulipifera L.: Rare.

The seed is 5 × 2.5 × 1.5 mm, flattened-ovoid, with a transversely wrinkled surface and a basal heteropyle. Figure 37.

PLATANACEAE

Platanus occidentalis L.: Numerous.

The spherical receptacles are 5 to 10 mm in diameter and have a pitted surface indicative of the insertions of the individual fruits. Associated 10 to 20 cm-broad leaves have three to five shallowly pointed, acuminate lobes with teeth scattered along their margins. Venation is actinodromous or palinactinodromous and semicraspedodromous. Many specimens have stout, 5–10 cm long petioles. Figures 3, 62.

ROSACEAE

Rubus sp.: Several.

The pyrene 3.5 × 2.5 mm, compressed ovoid to oblongoid. The lateral surfaces are marked by deep pits which form a reticulum. Identification to species on pyrene characters is not possible in *Rubus*. Figure 39.

Crataegus sp.: Several.

The seeds are about 6.5 × 3.8 mm, rough-surfaced, rounded on one face and bearing three ridges on the other. Identification to species is not possible with seeds of *Crataegus*. Figure 40.

Prunus nigra Ait.: Rare.

The endocarp is 14 mm in diameter, flattened spheroidally, with a low ridge along one side. Figure 41.

STAPHYLEACEAE

Staphylea trifolia L.: Several.

The seeds are about 5.5 × 5.2 × 4.1 mm, slightly compressed ellipsoid to subglobose. The smooth surface and distinct hilar scar with multiple vascular traces are characteristic of *Staphylea*. Figure 42.

ACERACEAE

Acer L. sp.: Rare.

The wingless fruit is 8 × 6 × 2 mm, compressed ellipsoid. A flattened area denotes the point of attachment to the other fruit. The surface is marked by reticulate venation. Figure 43.

Acer saccharum Marsh.: Rare.

The 7 to 10 cm-long, deeply palmate leaf has a cordate base and three to five pointed lobes. Primary venation is basal perfect actinodromous and secondary venation is semicraspedodromous. Figure 63.

VITACEAE

Vitis labrusca L.: Several.

The seeds are about 6 × 4 × 2 mm, oblong in frontal section and elliptic in transverse section, not rounded-triangular. The body constricts quickly from broad shoulders to a cuspidate, not acuminate, apical beak. This suite of characters distinguishes *Vitis labrusca* from other species in northeastern North America. Figure 44.

Parthenocissus Planch. sp.: Several.

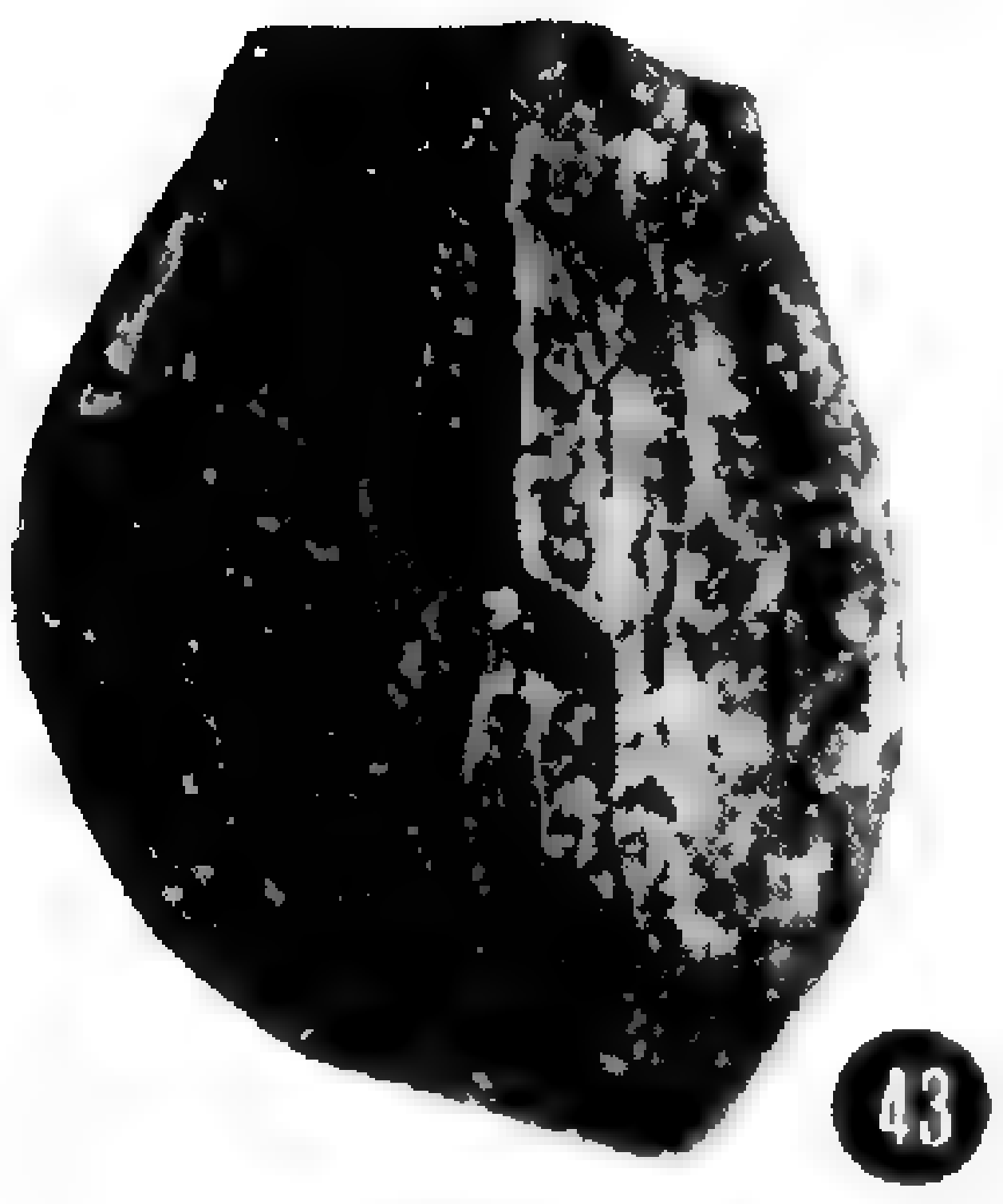
The seeds are about 4.2 × 3.7 × 2.7 mm, with a dorsal chalaza and narrow ventral infolds, globose, sometimes with a rounded-triangular transverse section. The seed is too short and broad to be *Vitis*, and the ventral infolds are too narrow for *Ampelopsis*. Figure 45.

TILIACEAE

Tilia americana L.: Several.

The capsule is spherical to ellipsoid, about 6 mm in diameter, with five thin sutures and a slight apical point. Leaves are 10 to 15 cm

Figures 43–57. Specimen identifications as indicated; further discussion in the text. **43.** *Acer* sp. Fruit without wing. ×3.4. **44.** *Vitis labrusca*. Seed. ×4. **45.** *Parthenocissus* sp. Seed. ×4. **46.** *Tilia americana*. Capsule. ×3.5. **47.** *Viola* sp. Capsule. ×5. **48.** *Nyssa sylvatica*. Endocarp. ×4. **49.** *Cornus alternifolia*. Endocarp. ×4. **50.** *Cornus amomum*. Endocarp. ×5. **51.** *Cornus drummondi*. Endocarp. ×3.6. **52.** Ericaceae, genus indet. Capsule ×3.5. **53.** *Sambucus pubens*. Seed. ×6. **54.** *Sambucus canadensis*. Seed. ×6. **55.** *Ambrosia trifida*. Achene. ×5. **56.** *Ambrosia artemisiifolia*. Achene. ×4. **57.** *Helianthus* cf. *decapetalus*. Achene. ×2.5.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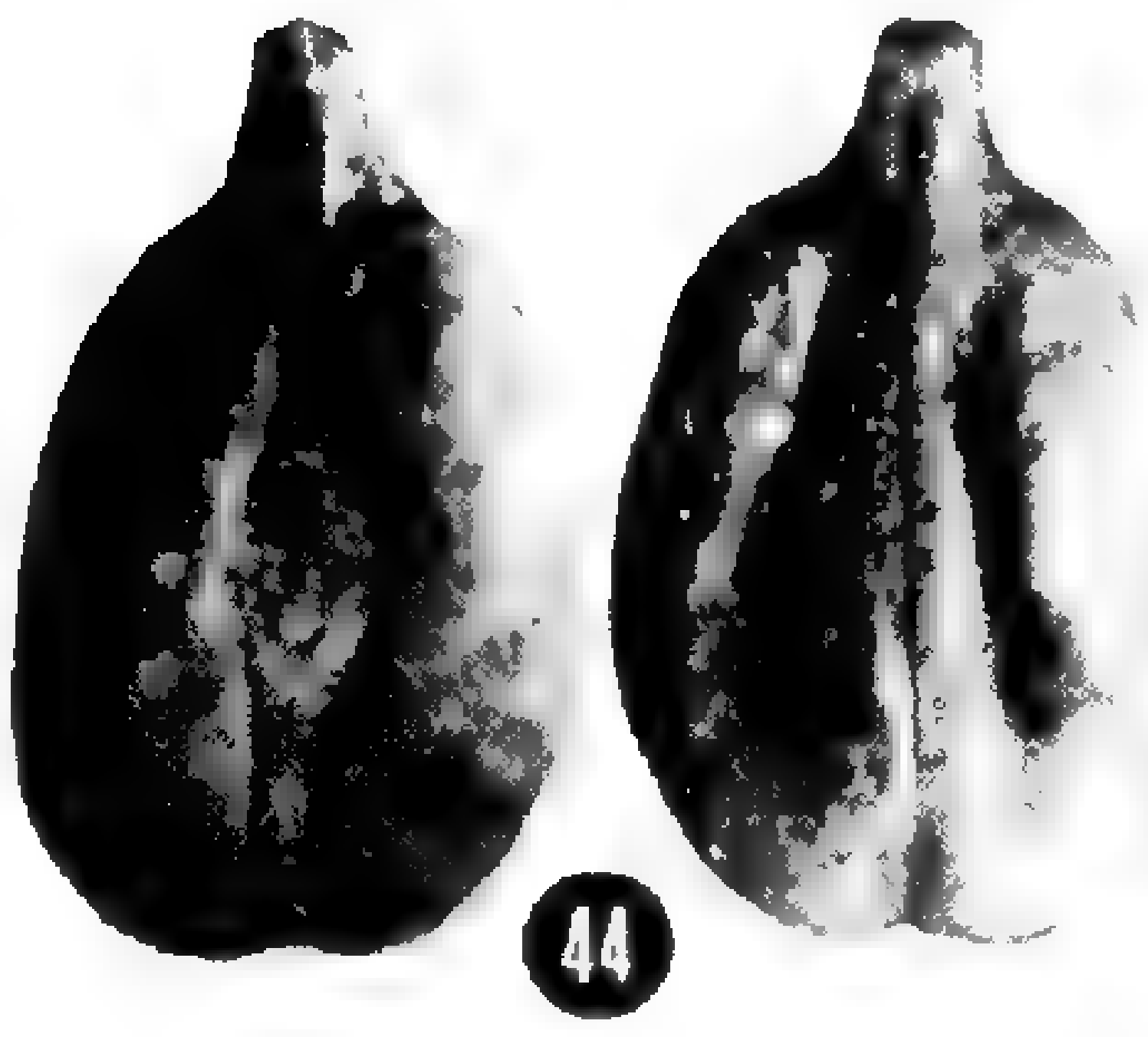
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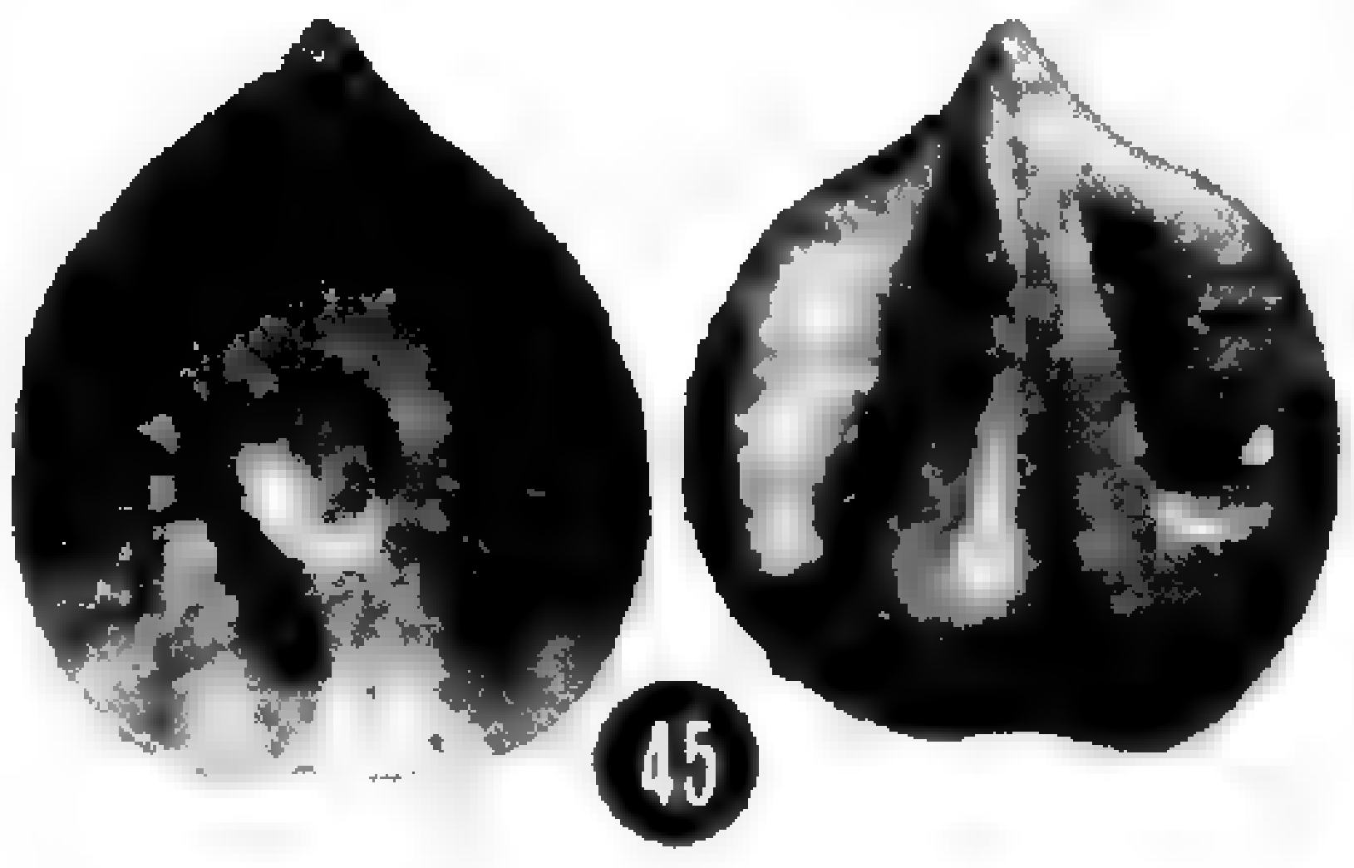
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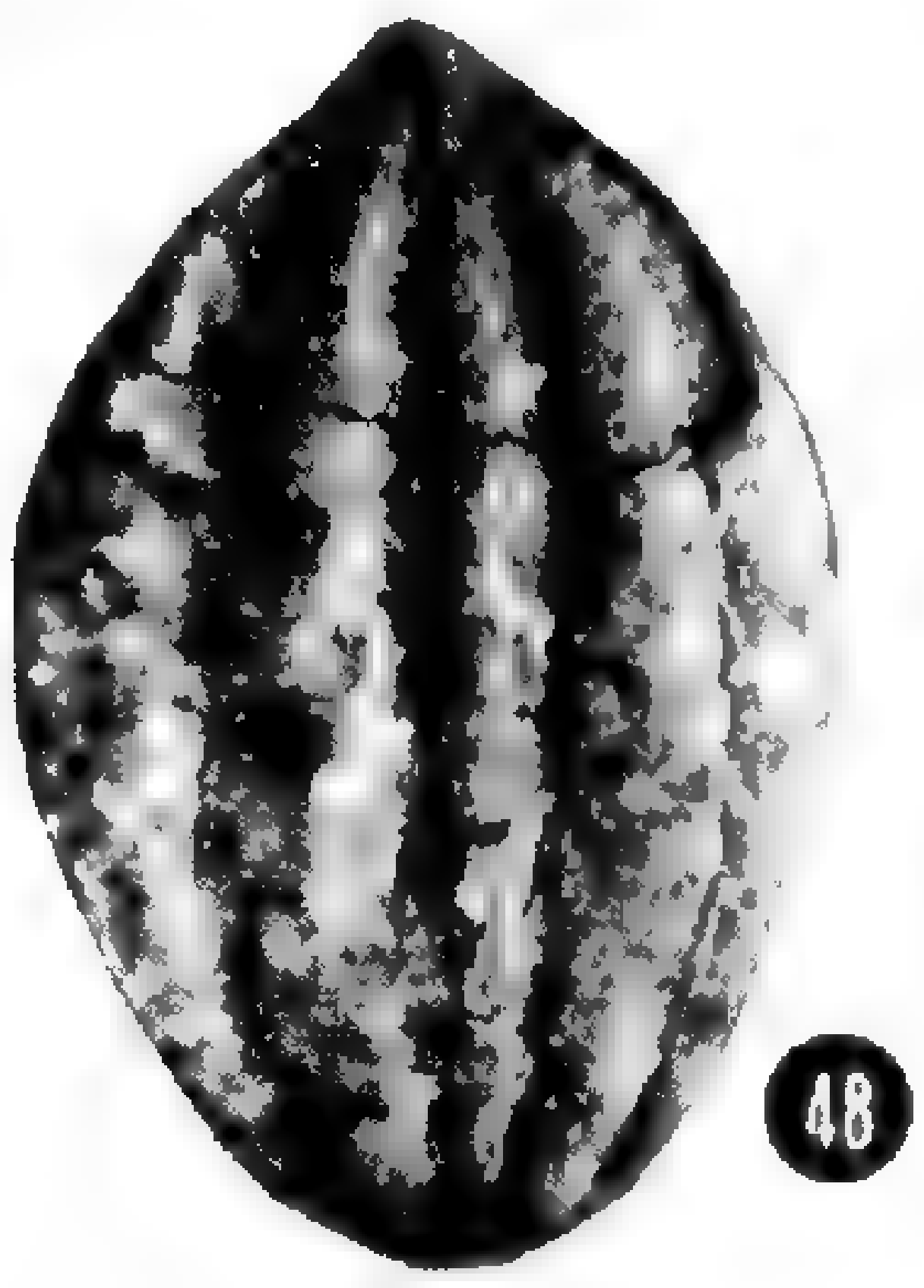
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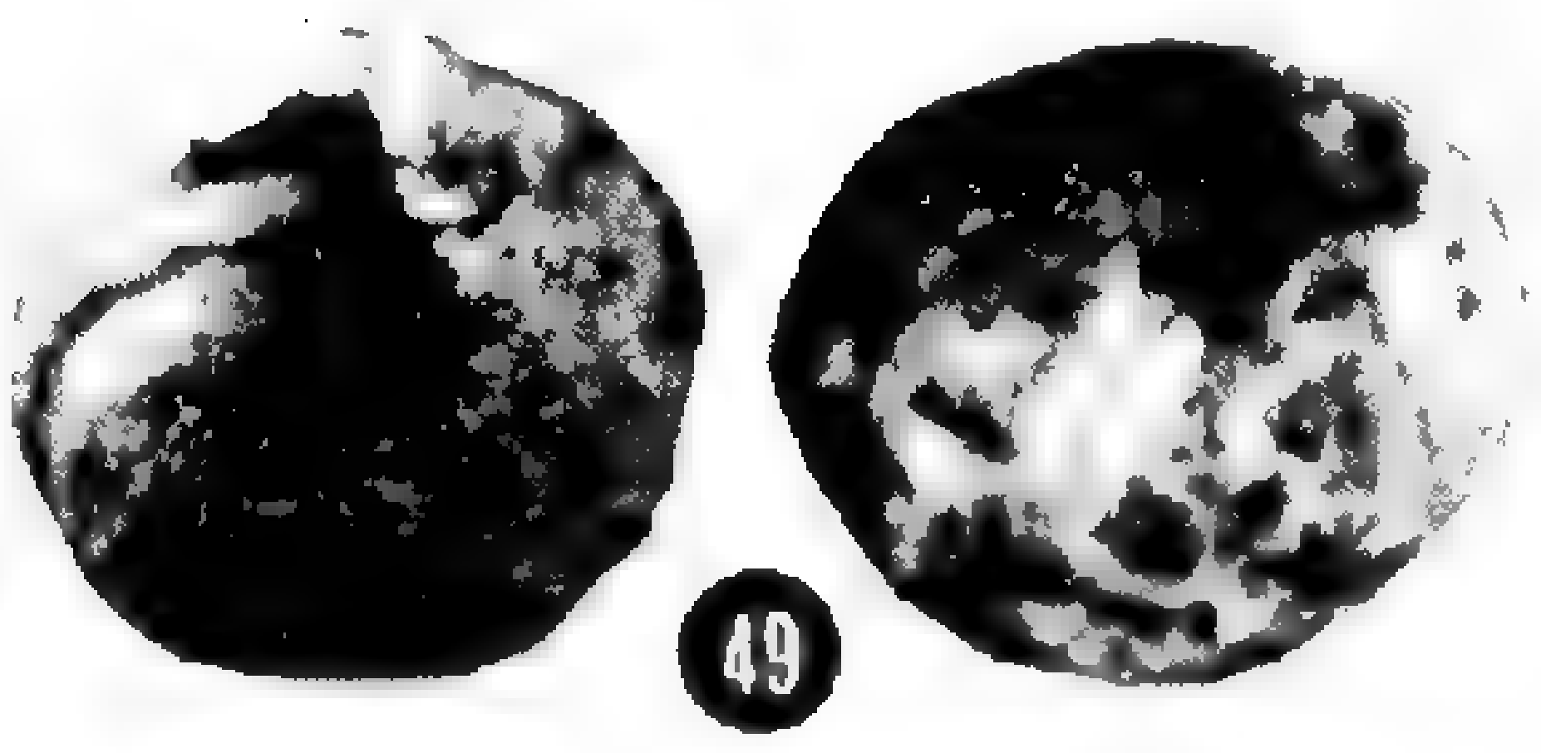
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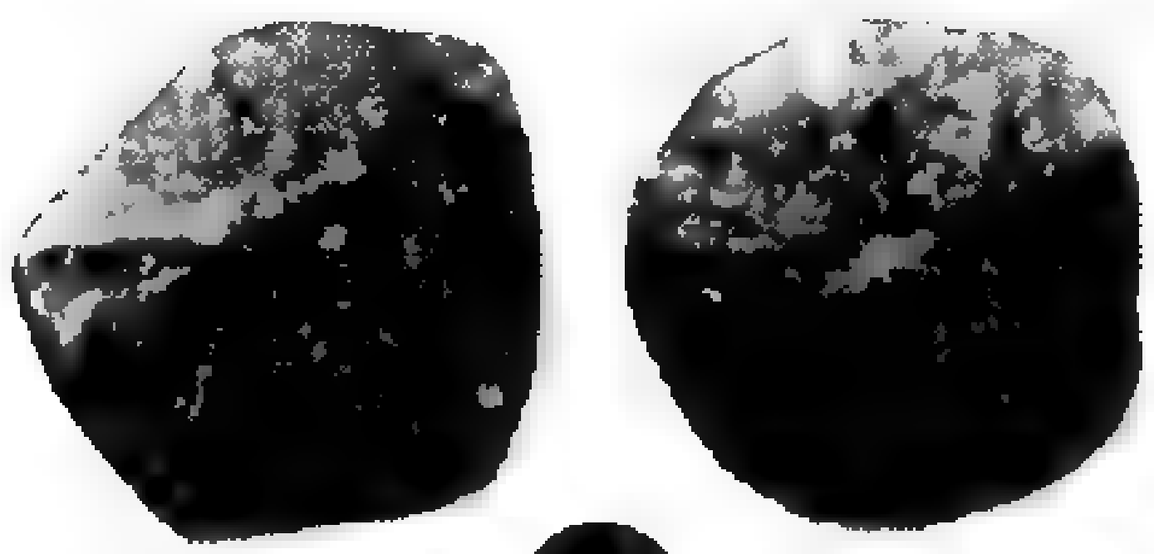
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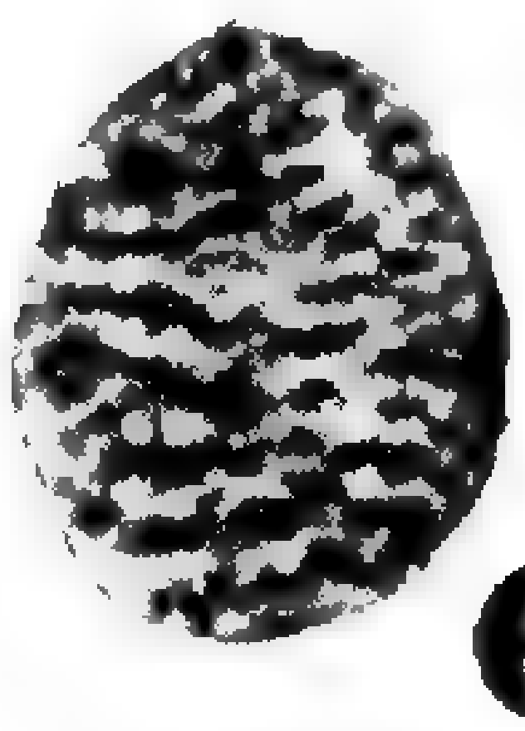
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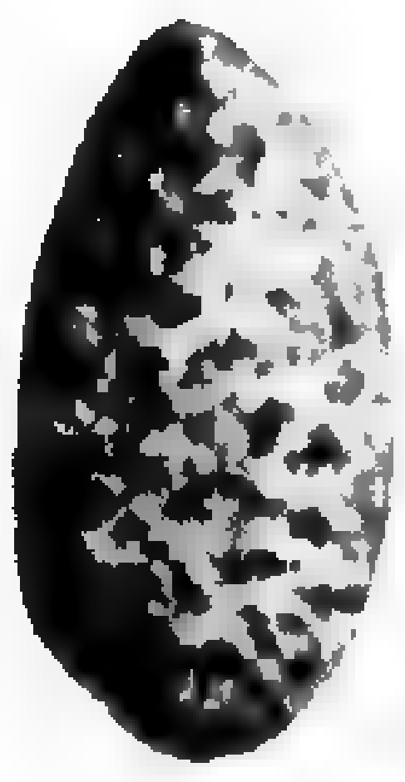
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long; obovate in shape with a cordate base and a cuspidate apex. The basal perfect actinodromous primary venation and craspedodromous secondary venation lead to a finely toothed margin. The fruit bracts are 7 to 10 cm long by 1.5 to 2.5 cm broad with pinnate, reticulodromous to weakly brochidodromous venation and a basally attached fruit stalk. Figures 47, 64, 65.

VIOLACEAE

Viola sp.: Rare.

The three-locular papery capsule conforms to that of *Viola,* but has no characters by which it can be identified to species. Figure 47.

NYSSACEAE

Nyssa sylvatica Marsh.: Several.

The 7 × 5 × 3 mm-endocarp is marked by ten to twelve prominent, rounded ridges with intervening grooves on each face and a distinctive germination valve. Figure 48.

CORNACEAE

Cornus alternifolia L.: Several.

The globose endocarp is about 3.7 mm in diameter, with surficial grooves containing veins. The species is distinguished by the large, irregularly-shaped apical pit. Figure 49.

Cornus amomum Mill.: Several.

The obliquely ellipsoid endocarp is about 4 × 3 × 3 mm, and marked by very prominent ridges. Figure 50.

Cornus drummondi Meyer.: Rare.

The ellipsoid endocarps are about 4 × 3 × 3 mm and are marked by deep circumferential grooves. These are too large to be *C. rugosa* Lam. which has a circumferential groove, but is globose. These are also distinct from *C. racemosa* Lam., which is obliquely ellipsoid and has a circumferential line, rather than a groove. Figure 51.

ERICACEAE

Genus indeterminable: Numerous.

The capsules are about 3.7 mm in diameter, spherical to obovoid with flat to depressed centers, five-valved, and bear very small seeds.

Unopened capsules display moderate to faint thickenings over the valve sutures. While the last characteristic suggests *Lyonia* Nutt., the thickenings are not pronounced (perhaps due to erosion prior to fossilization), and we cannot exclude the possibility that these capsules belong to *Andromeda* L. or *Chamaedaphne* Moench. Figure 52.

CAPRIFOLIACEAE

Sambucus pubens Michx.: Several

The 2.5 × 2 × 1 mm seed is elliptic to oblong in frontal section and compressed rounded triangular in transverse section, the surface marked by transverse wrinkles. See note below. Figure 53.

Sambucus canadensis L.: Several.

The seeds are 2.8 × 1.5 × 1 mm, slightly longer and narrower than those of *S. pubens*, but similar in shape and surface pattern. It is possible that these seeds of *Sambucus* are from the same species, but they appear to agree with the two species cited. Figure 54.

COMPOSITAE

Ambrosia trifida L.: Rare.

The achene is 8 to 12 mm long, otherwise similar to that of *A. artemisiifolia* from which it is distinguished by its larger size. Figure 55.

Ambrosia artemisiifolia L.: Numerous.

The achene is 4 to 5 mm long, irregular to obovoid, with four to seven spikes surrounding the central subulate apical beak. The beak is 1 to 2 mm long and exceeds the spikes. Figure 56.

Helianthus cf. **decapetalus** L.: Rare.

The achene is 5 mm long and 2 mm wide, ovoid and flattened with an apical notch and a striate surface characteristic of *Helianthus* species. Figure 57.

DISCUSSION

All the taxa on the species lists (Table 1) are members of the flora of lowland southern Connecticut. This finding is consistent with previous work demonstrating that the vegetation of southern Connecticut has changed little during the past 2800 years, excluding the

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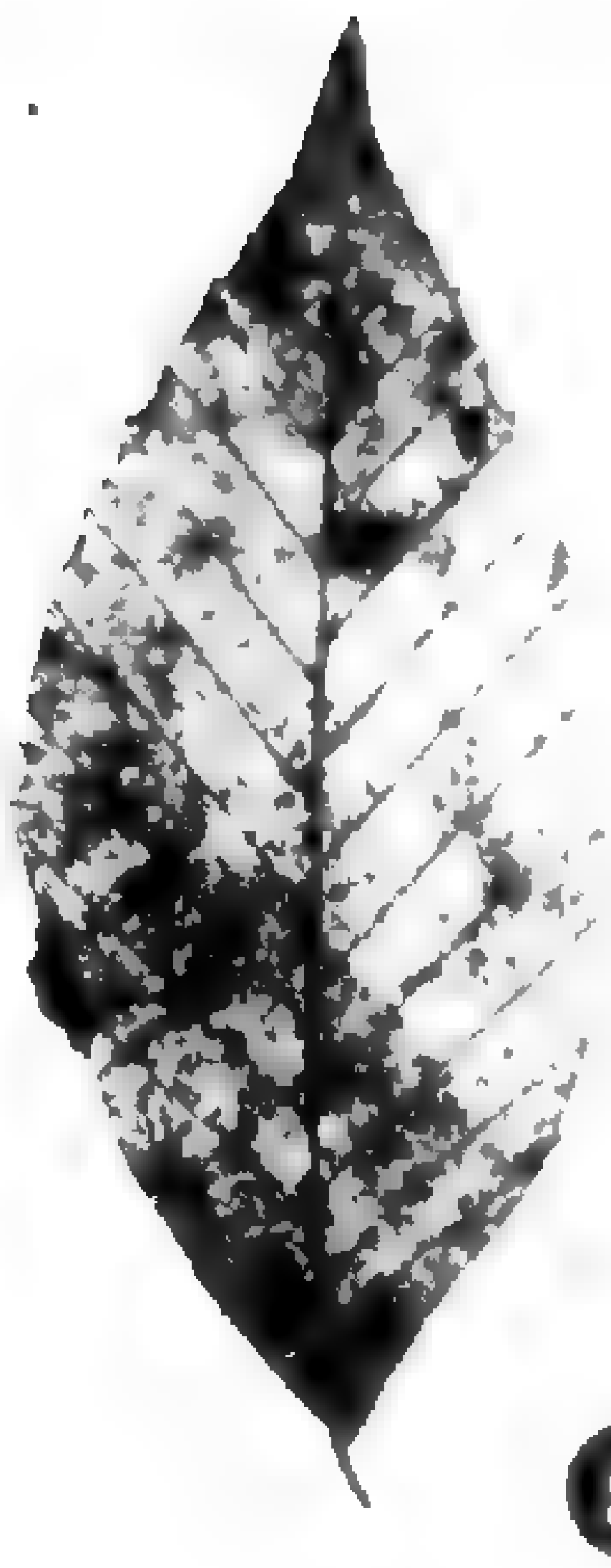

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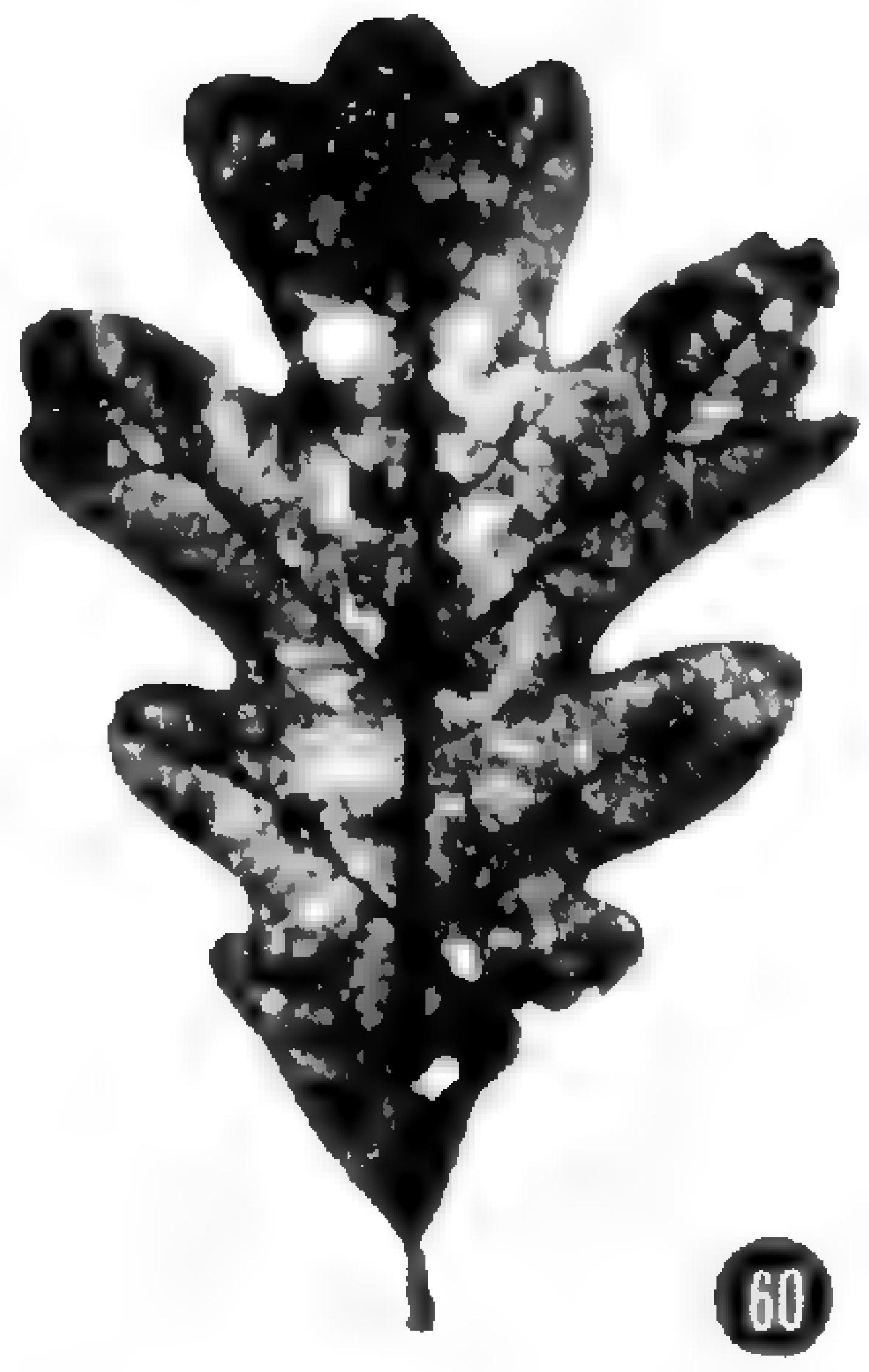

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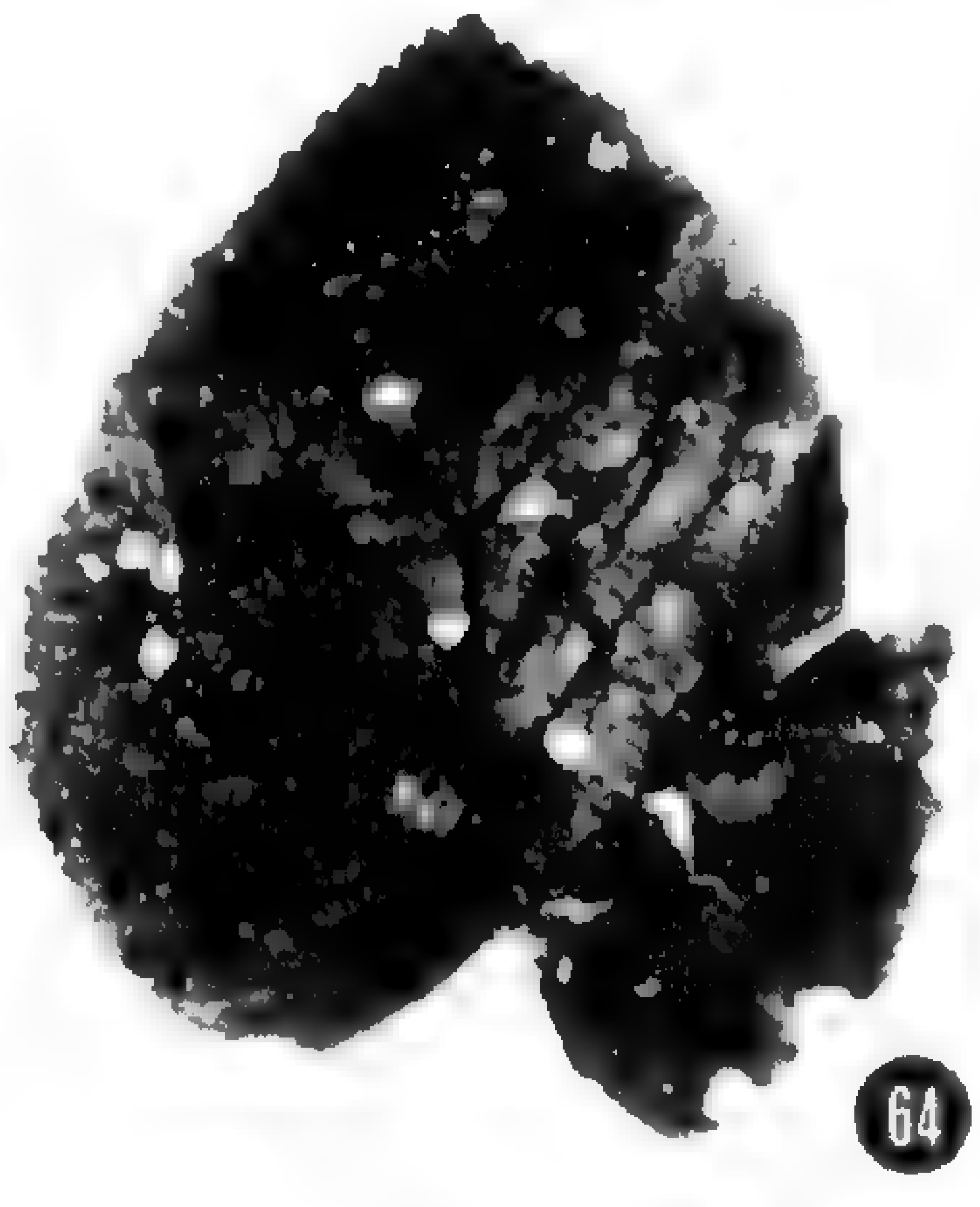

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effects of European settlement in the past 350 years, and correlates well with the pollen record (Davis, 1969b, 1976).

Noteworthy taxa include *Staphylea trifolia,* which has not previously been reported from the Holocene of New England, and *Liriodendron tulipfera,* whose pollen is rarely preserved in lake sediments (T. Webb, pers. comm.).

The flora includes plants which grow in a variety of habitats: aquatic plants of still or slow-moving water such as *Ceratophyllum echinatum, Brasenia schreberi, Zannichellia palustris,* and *Ranunculus trichophyllus;* marsh plants such as species of Cyperaceae and *Sparganium;* levee and flood plain dwellers such as *Platanus occidentalis, Nyssa sylvatica* and *Alnus* sp.; forest trees which prefer well drained soils, such as *Acer saccharum, Fagus grandifolia* and *Quercus alba;* and species which live in open sunny areas such as *Helianthus* and *Ambrosia* (Braun, 1950; Fowells, 1965; Fernald, 1970).

This floral variety is not surprising, given that macrofossils may be transported up to a few kilometers by rivers (Burrows, 1980; Drake and Burrows, 1980; Spicer, 1981). The deposit of fruits and seeds probably represents several different plant associations growing along the banks or on the floodplain of the Quinnipiac River. Some fossils show signs of wear, evidence of relatively long distance transport: seeds of Pinaceae lack wings, fruits of *Acer* lack wings, and the *Alnus* aments are in poor condition. The excellent condition of many of the fossils from the same lens, however, suggests that they were not transported long distances before being deposited. Many fruits have relatively fragile structures intact, including bristles on *Scirpus* species and *Dulichium arundinaceum* and styles on *Zannichellia palustris* and *Carex lupulina.* Additionally, entire leaves were very common in the leaf mats studied.

Figures 58–65. Specimen identifications as indicated; further discussion in the text. **58.** *Smilax* sp. Leaf (reflected light). ×0.5. **59.** *Fagus grandifolia.* Leaf (transmitted light). ×0.5. **60.** *Quercus alba.* Leaf (transmitted light). ×0.5. **61.** *Quercus* cf. *coccinea.* Leaf fragment (reflected light). ×0.33. **62.** *Platanus occidentalis.* Leaf (reflected light). ×0.125. **63.** *Acer saccharum.* Leaf (transmitted light). ×0.5. **64.** *Tilia americana.* Leaf (transmitted light). ×0.5. **65.** *Tilia americana.* Fruit bract (transmitted light). ×0.5.

ACKNOWLEDGMENTS

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PEABODY MUSEUM OF NATURAL HISTORY
AND DEPARTMENT OF BIOLOGY
OSBORN MEMORIAL LABORATORY
YALE UNIVERSITY
P.O. BOX 6666
NEW HAVEN, CT 06511

POLLINATION BIOLOGY OF *PRIMULA LAURENTIANA* (PRIMULACEAE) IN MAINE

CHRISTOPHER S. CAMPBELL, NORMAN C. FAMOUS,
AND MICHAEL G. ZUCK

ABSTRACT

In eastern Maine the brightly colored flowers of *Primula laurentiana* Fern. produce no nectar; their faint but pleasant scent is strongest at the center of the corolla limb in a UV-reflecting, yellow ring called the "bird's eye." During our observations, six species of insects visited the flowers, the most important being the syrphid *Helophilus groenlandicus* (O. Fabricus) (Syrphidae). Since *P. laurentiana* is self-compatible, long-homostylous, and its stigmas are receptive when the introrse anthers dehisce, pollen-gathering by insects must lead to some self-pollination. Pollen adhering to pollinators' heads may effect cross-pollination during their flower-constant forays. This breeding system of facultative autogamy is concordant with the relatively low pollen-ovule ratio of about 130 to 1.

Key words: *Primula laurentiana, Helophilus groenlandicus,* pollination, homostyly, UV light, pollen-ovule ratio, eastern Maine

Plant biologists have long held a special interest in the genus *Primula* because many of the species are heterostylous, i.e., individuals differ reciprocally in stamen and style length (Ganders, 1979). Heterostyly and the associated system of intramorph incompatibility have stimulated numerous studies of the floral morphology, breeding systems, genetics and pollination of several Old World species of the genus (*see* references in Ganders, 1979). Most of these studies have also dealt with homostyly, a floral condition evolutionarily derived from heterostyly and involving the juxtaposition of anthers and stigmas. Homostylous plants are generally self-compatible and of two kinds. Long homostyles combine long styles with anthers positioned high in the corolla. Short homostyles, the rare kind, have short styles and low anthers.

Primula laurentiana, the bird's-eye-primrose, is a scapose, perennial calciphile of ledges, cliffs and meadows in northeastern North America (Scoggin, 1979). South of about 48°N it is relatively uncommon (Famous and Campbell, 1984). We report the first work on the pollination biology of this species. Through field and laboratory studies of natural populations on Great Wass Island in eastern Maine, we have attempted to (1) determine the floral attractants and rewards for pollinators, and (2) relate these floral characteristics to the pollinator fauna.

MATERIALS AND METHODS

We observed bird's-eye-primrose plants and their insect visitors throughout the flowering season in 1983 and returned later to collect fruit from marked individuals. We focused on several fairly dense populations totalling about 10,000 individuals located on the southern headlands of Great Wass Island (Beals Township, Washington County). Voucher specimens of the three major pollinators were deposited in the insect collection of the Department of Entomology at the University of Maine at Orono.

To determine the source of the floral odors, we followed a method of Faegri and van der Pijl (1979). We divided 30 corollas into the limb, the yellow center (the bird's-eye) and the tube, placed these parts into three separate small glass vials, and then three people sniffed the vials and recorded their perceptions. To document the appearance of *Primula* flowers in ultraviolet (UV) light, we photographed the same inflorescence in normal light and then through a filter (Kodak Wratten 18A), which allows passage of UV light.

We fixed flowers in FPA (formalin 5: propionic acid 5: 50% ethanol 90) and followed a standard dehydration in a graded alcohol series, embedding in paraffin, sectioning with a rotary microtome at 12μm and staining with safranin and fast green.

To determine pollen-stigma compatibility, we completely enclosed 11 plants in cages constructed of fine-mesh aluminum screening from before to after anthesis. We self-pollinated the flowers of seven plants with a camel's-hair brush and left the remaining plants undisturbed.

We used Dowrick's (1956) technique to determine stigma receptivity. First we emasculated caged flowers, selfed or crossed them and stored them with moistened paper in a small, closed jar. After 24 hours we fixed them in FPA and stored them in 70% ethanol. We then softened the gynoecia for two hours in 8N sodium hydroxide and stained them for four hours in 0.1% aniline blue in 0.1N potassium phosphate. We observed squashed gynoecia in a fluorescence microscope equipped with a Zeiss filter set 48 77 05 to determine if pollen tubes were present.

Pollen-ovule ratio estimates come from a count of all the pollen from one anther (multiplied by five) and all the ovules from the same flower for six different flowers. We measured scape lengths for flowering plants and a different sample of fruiting plants from the same population. For seed weight and dimensions we weighed 120 seeds collectively and measured length and width of 120 seeds lined up end to end and side by side respectively.

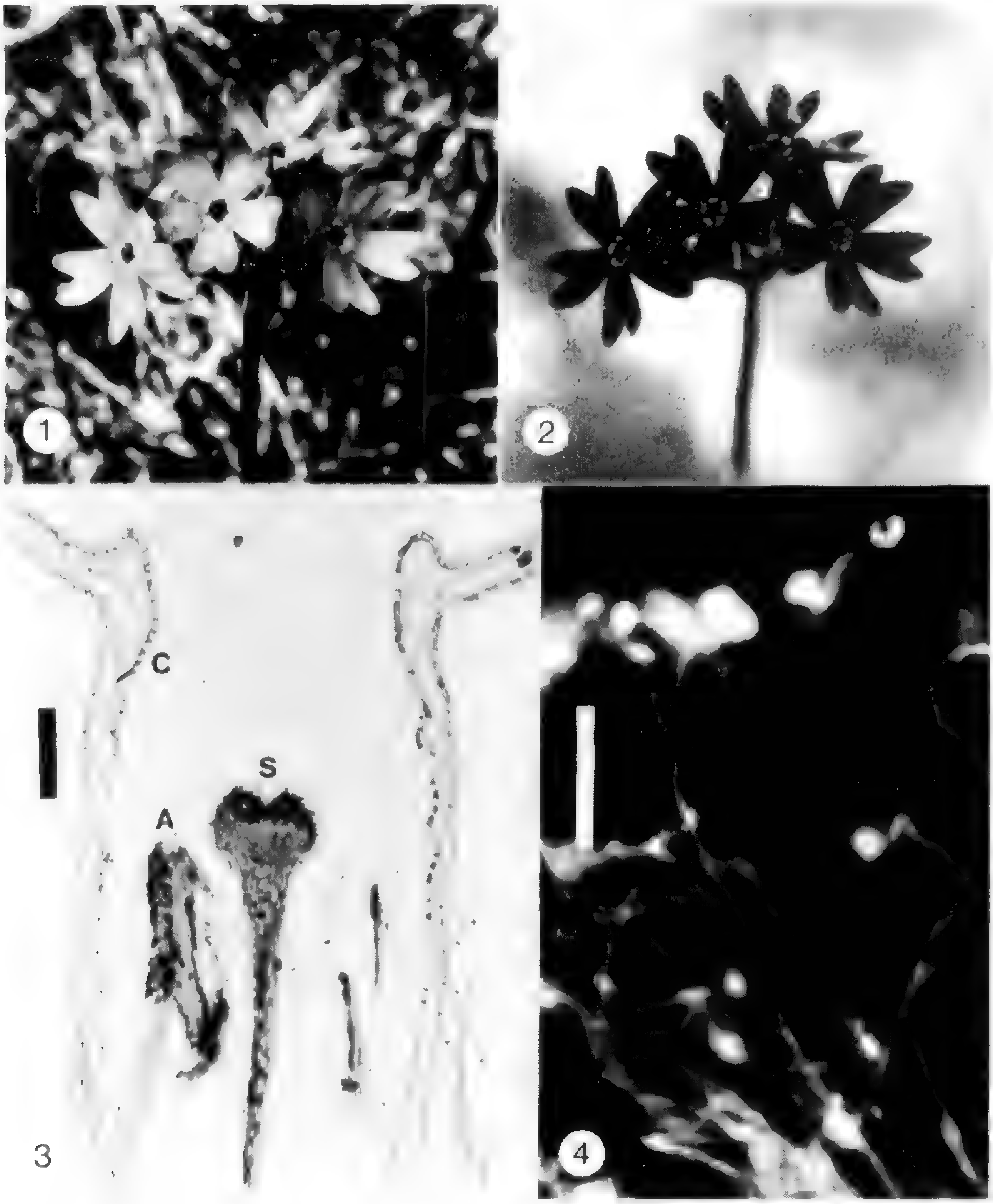
RESULTS AND DISCUSSION

In eastern Maine, *Primula laurentiana* flowers in May and June. The flowers (Figure 1) are about one cm broad, and the corolla, which is pink to lilac with a bright yellow spot at its center, is conspicuous in the full sun, wherein this species usually grows. The flowers are also conspicuous because of the paucity of other insect-pollinated flowers nearby. *Sedum rosea* (L.) Scop. and *Viola septentrionalis* Greene are the only entomophilous species that flower during the peak of flowering of *Primula* and which also grow intermixed with *Primula* on Great Wass Island.

Patterns of floral UV reflectance and absorption provide a potentially important pollinator cue, although it should be interpreted with caution (Kevan, 1983). In UV light the corolla limb of *Primula laurentiana* is strongly absorbing except for a ring at the center (Figure 2). This ring, which corresponds to a portion of the yellow bird's-eye of normal light, actually consists of five UV-reflecting bands alternating with the petals. Generally, yellow petals are UV-reflecting, but the usual pattern of UV-reflecting pigmentation surrounding the UV-absorbing center of flowers (Silberglied, 1979) is reversed in the bird's-eye-primrose. The corolla tube is almost always in shadow, making it dark at all wavelengths.

We do not know of any studies of the vision of *Helophilus,* the principal pollinator of *P. laurentiana* (see below). However, all four genera of the Diptera listed by Goldsmith and Bernard (1974) have either primary or secondary sensitivity maxima in the near UV. Hence the UV patterns of *Primula laurentiana* may guide its pollinators to the corolla tube.

Frohlich (1976) documented the striking contrast between many UV-absorbing flowers and their UV-reflecting background. The background vegetation in Figures 1 and 2 consists mostly of grasses



Figures 1 4. *Primula laurentiana.* **1.** Inflorescence in normal light, approx. life size; **2.** Same inflorescence in near-UV light; **3.** Photomicrograph of a portion of a sectioned flower showing the anther (A), corolla tube (C), and stigma (S). Bar scale – 500 μm; **4.** Fluorescence photomicrograph of self pollen and pollen tubes in a squashed stigma. Bar scale = 50 μm.

and sedges. The fact that this vegetation reflects UV light may facilitate pollinator recognition of *Primula* flowers.

The yellow rim of the corolla tube seemed to have the strongest fragrance to all three people in the scent comparisons. We found uniseriate, multicellular trichomes in the epidermis of the same part of the corolla. These structures appear to be secretory, but, according to Fahn (1979), such structures generally are not responsible for floral fragrances.

Our observation that the flowers of the bird's-eye-primrose are long homostylous—the stamens are located at the same level as or (more usually) slightly below the stigma near the top of the corolla tube (Figure 3)—is consistent with those of Fernald (1928) and Dorwick (1956). Our sections also do not reveal any prominent nectaries, nor could we detect with a 20× hand lens any nectar sources in living flowers. This lack of nectar leaves pollen as the major reward for pollinators.

During warm (above 12°C) dry and calm weather we noted six species of insects visiting bird's-eye-primrose flowers. Three of these—a butterfly, *Cynthia cardui* (L.) (Nymphalidae), a large fly, and a small syrphid fly—spent little time on *Primula* and did not appear to be effective pollinators. Two species of bumblebee (*Bombus*) and a syrphid (*Helophilus groenlandicus*) on the other hand, spent considerable time on the flowers (Table 1). Although we did record a similar total number of flowers visited by the syrphid and the two bumblebees, almost two-thirds of the flowers visited by the latter were on one foray. The syrphid, a circumboreal species, was clearly the most consistent flower visitor. These flies deliberately and repeatedly probed the corolla tube while sitting on the limb. We opened the gut of one individual collected at the end of a 10-flower, four-minute foray and found an abundance of *Primula* pollen. With their short proboscis, syrphids are generally limited to the consumption of pollen rather than nectar (Faegri and van der Pijl, 1979). Both bumblebees and this syrphid were flower constant: they did not alight on non-*Primula* flowers during their forays on *Primula*. *Helophilus groenlandicus* did visit *Sedum rosea,* but only after the peak of *Primula* anthesis.

Controlled self-pollinations show bird's-eye-primrose to be self-compatible. Self pollen germinates freely (Figure 4) and grows to the ovules within 24 hours. In contrast, in self-incompatible pollinations in *Primula obconica,* the pollen tube rarely penetrated the stigma in 24 hours (Dowrick, 1956). Foreign pollen performed similarly to self pollen in *P. laurentiana.*

The stigma is usually green when the anthers dehisce but later turns dark red. Pollen tubes penetrate the stigma before and after it

Table 1. Pollinator observations of *Primula laurentiana*

Total days of observation (12 May–12 June, 1983)	10
Total hours of observation	38.5

Pollination Activity	*Helophilus groenlandicus*	Two Species of *Bombus*
Total number of forays[a]	101	13
Mean (S.D.; range) flowers/foray	7.6 (7.2; 1–44)	51.9 (117.4; 4–439)
Mean (S.D.; range) seconds/flower	7.4 (5.9; 2–42)	2.6 (1.1; 3–6)
Total flowers visited	768	675
Total minutes on flowers	94.7	29.2

[a] A foray is one uninterrupted sequence of floral visitations by one individual insect.

turns red. Protandry, and its potential for outbreeding, therefore does not occur in *Primula laurentiana*. Since the flowers open just before the anthers dehisce, protogyny seems unlikely.

Homostyly, the simultaneous maturity of anthers and stigmas, and the fact that the stamens are introrse (Figure 3) ensure that the syrphid and bumblebees must self-pollinate bird's-eye-primrose during their often protracted pollen-gathering visits. Our estimates of pollen-ovule ratios (133± 15) are close to Cruden's (1977) mean value (168.5 ± 22.1) for his breeding system of facultative autogamy. We don't know how much pollen adheres to pollinators' bodies and thereby effects cross-pollination.

In general, caged *Primula laurentiana* sets seed when artifically selfed or when not touched. How does fertilization occur in these untouched plants? We could not find within any flowers small insects such as thrips or small beetles, which might have passed through the cage and which have been suggested as possible pollinators in other species of *Primula* (Woodell, 1960). We suspect that the wind blows the flowers against the cages and forces the anthers against the stigma. We don't know if such "wind" pollination occurs normally.

Mean scape length increases significantly ($t = 12.96$, $P > 0.01$; Zar, 1974) between anthesis (8.7 ± 2.8 cm) and fruit maturation (15.7 ± 2.8 cm). The seeds are light (0.0607 mg) and small (0.473 × 0.653 mm). The erect capsules open apically, and the seeds are gradually released in a "salt shaker" fashion. They do not show obvious adaptations for wind or animal dispersal, nor do they float. Self-compatibility would facilitiate the establishment of new populations from individuals isolated after long-distance dispersal.

Primula laurentiana is morphologically very similar to *P. farinosa* L., the bird's-eye-primrose of the mountains of Europe (C.S.C., personal observation of plants in Austria). *Primula laurentiana* is octoploid or hexaploid (Dorwick, 1956; Vogelmann, 1960) and homostylous, as in some other polyploid Primulas (Vogelmann, 1960; Dowrick, 1956). Polyploidy may actually have provided a greater opportunity for the recombinations necessary to produce homostyly (Dowrick, 1956). *Primula farinosa* is characterized by the constrasting suite of ancestral character states: diploidy, heterostyly and self-incompatibility.

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DEPARTMENT OF BOTANY AND PLANT PATHOLOGY
UNIVERSITY OF MAINE
ORONO, MAINE 04469

THE CYTOGEOGRAPHY OF *CHRYSOPSIS MARIANA* (COMPOSITAE:ASTEREAE): SURVEY OVER THE RANGE OF THE SPECIES

JOHN C. SEMPLE AND C. C. CHINNAPPA

ABSTRACT

Chromosome numbers determined from 49 populations of *Chrysopsis mariana* (L.) Ell. ranged from diploid to octoploid: $2n = 8$, $2n = 16$, $2n = 24$, $2n = 32$ respectively. Seedlings from one $6x$ population had 5–9 small supernumerary chromosomes. These counts plus 8 previously reported counts indicate an allopatric distribution pattern of cytotypes throughout the range of the species. All cytotypes were found in Florida, whereas only hexaploids occurred in other parts of the range. Diploids occurred in two disjunct areas of Florida. Tetraploids and octoploids were found only in the northeastern portion of the Florida peninsula.

Key Words: cytogeography, polyploidy, goldenaster, *Chrysopsis*, Astereae

INTRODUCTION

Chrysopsis mariana (L.) Ell. is the most widely distributed species in this recently revised genus (Semple, 1981). The first chromosome number reported for this species was $2n = 24$ (Smith, 1966). Harms (1974) reported a meiotic count of $n = 12$ and postulated that the species was a tetraploid with base number of $x = 6$. Semple (1977) reported counts of $2n = 8$, $n = 12$, and $2n = 24$ and concluded that the base number was $x = 4$. Semple and Chinnappa (1980) reported the occurrence of an octoploid plant with $2n = 32$. The diploid karyotype was illustrated and described in Semple and Chinnappa (1980) along with karyotypes of the other species in the genus. The existence of the tetraploid race was noted by Semple (1981), but no locations or vouchers were cited. Field work during the last several years has resulted in an additional 49 populations being sampled. The chromosome number determinations and their geographic distributions are reported for the first time in this paper.

MATERIALS AND METHODS

Meiosis was observed in pollen mother cells (PMC's) prepared as follows. Capitulescence buds (heads) were fixed in the field in 3:1 absolute alcohol: glacial acetic acid, then stored in 70% EtOH under refrigeration until examined. Anthers were dissected out of florets removed from the heads and squashed in 1% acetic orcein stain under a coverslip coated with egg albumin in glycerin. Observations were made on fresh preparations. Permanent slides were made by floating off the coverslip with adhering cells in 10% acetic acid, then dehydrating in a 70%-95%-100% EtOH series before mounting on a clean slide with Euparol. Permanent slides remain in the possession of the first author.

Mitotic counts were determined from root tip cells prepared as follows. Achenes collected in the field were germinated in vermiculite in the greenhouse facilities at the University of Waterloo. Actively growing root tips were removed from seedlings, pretreated in 0.01% colchicine for 2 hrs., then fixed in Modified Carnoy's Fixative (4:3:1 / chloroform: absolute EtOH: glacial acetic acid, by volume) and stored without solution change at -4° C. Before squashing, root tips were hydrolized in 1N HCl for 30 min at 60° C. The meristematic tips were then squashed as above. Permanent slides were made as above.

RESULTS

Chromosome number determinations from seedlings and wild individuals from 49 populations are listed in Table I. A dozen diploid populations were found in Florida; four tetraploid populations were sampled in northeastern Florida; one octoploid population was sampled near the coast in northeastern Florida. Twenty-nine hexaploid populations were sampled from the southern and central portions of the range excluding Florida. Seedlings grown from achenes collected at one population in eastern Virginia were found to have varying numbers of small euchromatic supernumerary chromosomes ($2n = 24 + 5$–9 supernumeraries).

DISCUSSION

In total, 57 populations of *Chrysopsis mariana* have been sampled cytologically, including those reported previously. The geographical distribution of the cytotypes is illustrated in Figure 1. The range of the species is indicated by broken lines (Semple, 1981). Although some areas of the range are sparsely sampled, the overall distribution pattern of cytotypes is clear. Based on a much smaller sample of published and unpublished counts, Semple (1981) noted

Table 1. Chromosome number determinations and voucher data for *Chrysopsis mariana* from the United States. All collections by Semple & Chmielewski unless otherwise indicated: Bt = L. Brouillet, C = J. Canne, S = J. Semple, S & S = J. & B. Semple. Vouchers in WAT.

COUNT 2*n* =	COLLECTION LOCATION AND VOUCHER DATA (WAT)
4_{II}	**Florida.** Osceola Co.: N of Davenport, *S 5344.*
8	**Florida.** Calhoun Co.: W of Clarksville, *S & Godfrey 3105.* Lafayette Co.: S of Cooks Hammock, *S & S 7444.* Liberty Co.: W of Bloxham, *S & S 7424.* Madison Co.: US-221, 4.9 mi N of county line, *S, Bt & C 3914.* Pasco Co.: US-301, just N of county line, *S & S 5417.* Sumter Co.: FL-44, 3.8 mi E of county line, *S, Bt & C 3976.* Suwanee Co.: SE of Wellborn, *S & S 7451.* Taylor Co.: W of Hampton Springs, *S & S 7441.* Wakulla Co.: N of Ivan, *S & S 7426;* N of Panacea, *S & S 7439.* Washington Co.: E of Bonifay, *S & Godfrey 3181.*
8_{II}	**Florida.** Levy Co.: N of Inglis, *S, Bt & C 3958.* Putnam Co.: FL-19, 0.5 mi N of Oklawaha River, *S, Bt & C 3958.*
16	**Florida.** Duval Co.: SE of Callahan, *S & S 7546.* St. Johns Co.: W of St. Augustine, *S & S 7544.*
12_{II}	**South Carolina.** Chesterfield Co.: S of Pageland, *S, Brammall & Hart 3036.* Williamsburg Co.: N of Rhems, *6124.*
24	**Alabama.** Etowah Co.: N of Attalla, *6302.* Randolph Co.: N of Wedowee, *6313.* Tuscaloosa Co.: Northport City, *6369.* Wilcox Co.: S of Millers Ferry, *6360.* **Florida.** Gadsden Co.: E of Chattahoochee, *S & Godfrey 3284;* US-90 6.3 mi W of county line, *S & Godfrey 3186.* Jackson Co.: Marianna, *S & Godfrey 3183.* **Georgia.** Coffee Co.: SE of Broxton, *S & S 7413.* Evans Co.: S of Claxton, *S & S 7560.* Lowndes Co.: W of Valdosta, *S & S 7418.* White Co.: N of Robertstown, *6214.* Wilcox Co.: NW of Abbeville, *S & S 7411.* **Kentucky.** Whitley Co.: KY-92 2.8 mi E of county line, *S, Brammall & Hart 2994.* **Mississippi.** Alcorn Co.: E of Strictland, *6348.* Rankin Co.: US-49 3 mi N of road to Star, *S, Bt & C 3808.* **New Jersey.** Burlington Co.: N of Chatworth, *6258.* Cape May Co.: NE of Dennisville, *6253.* **North Carolina.** Catawba Co.: S of Millerville, *S, Bt & C 4076.* Henderson Co.: W of Chimney Rock, *S, Brammall & Hart 3029.* Transylvania Co.: E of Connestee, *6175.* Wayne Co.: NW of Cliffs of Neuse State Park, *6044.* Wilkes Co.: McGrady, *S, Bt & C 4081.* **Ohio.** Scioto Co.: Shawnee State Forest, *S, Brammall & Hart 2983.* **South Carolina.** Chester Co.: SE of Chester, *6097.* Richland Co.: NW of Columbia, *S, BT & C 4067.* **Tennessee.** Morgan Co.: W of Rugby, *S, Brammall & Hart 3006.* **Virginia.** Culpepper Co.: NW of Lignum, *5951.* Madison Co.: SW of Culpepper, *5941.* Middlesex Co.: NE of Harmony Village, *5975.*
24 + 5–9 supernumeraries	**Virginia.** Essex Co.: SE of Chance, *5967.*
32	**Florida.** Flagler Co.: N of Bunnell, *S 7535.*

that hexaploids were by far the most widely distributed cytotype and that there were a few counts of other cytotypes from populations in Florida. The new data reported in this paper indicate that within Florida, hexaploids are in fact restricted to a small area northwest of Tallahassee. This area is not floristically like areas to the south (R. K. Godfrey, pers. comm.). Based on the present sample, we interpret the hexaploid count reported from the Merritt Island area of Florida (Semple, 1977; indicated in Figure 1 by an open circle) to be a possible F_1 hybrid between a tetraploid and an octoploid, both of which are now known to occur in that area. Otherwise, the count indicates that there is a disjunct population of hexaploids in that part of Florida.

The new data also indicate that within Florida, the $2x$, $4x$ and $8x$ cytotypes are allopatric. Furthermore, the distribution of these cytotypes fits the general pattern of distribution in Florida of the $x = 5$ species for the genus *Chrysopsis* as a whole. The $x = 5$ diploids are distributed in three patterns (Semple, 1981): 1) only in the panhandle area (e.g., *C. lanuginosa* Small); 2) only in the peninsula area (e.g., *C. latisquamea* Pollard); or 3) as disjunct panhandle and peninsula populations (e.g., *C. linearifolia* Semple). Several of these general patterns are represented in *C. mariana.* The diploids show disjunction, the last type of distribution pattern. Nine $2x$ populations occur in the Florida panhandle area and three were found in the central peninsula area. Tetraploids were found only in the northern peninsula area between the two groups of diploids, and thus have the second distribution type. The two $8x$ samples came from near the Atlantic coast on, or north of, Merritt Island. The $8x$ plants are unusual in that they have very large heads for the species. Such plants occur only in eastern Florida and thus also have the second type of distribution pattern.

In conclusion, it appears that each cytotype is endemic to a particular part of Florida. One of these areas, the region northwest of Tallahassee, is the southern end of a broadly distributed floristic region and thus by chance the hexaploid race is much more broadly distributed than the other cytotype races of the species. The sample size within Florida, however, is relatively small, and a much larger sample may reveal some sympatry that is not indicated by the current data base. Geographic isolation and subsequent chance divergence were hypothesized to be major factors in the evolution of the

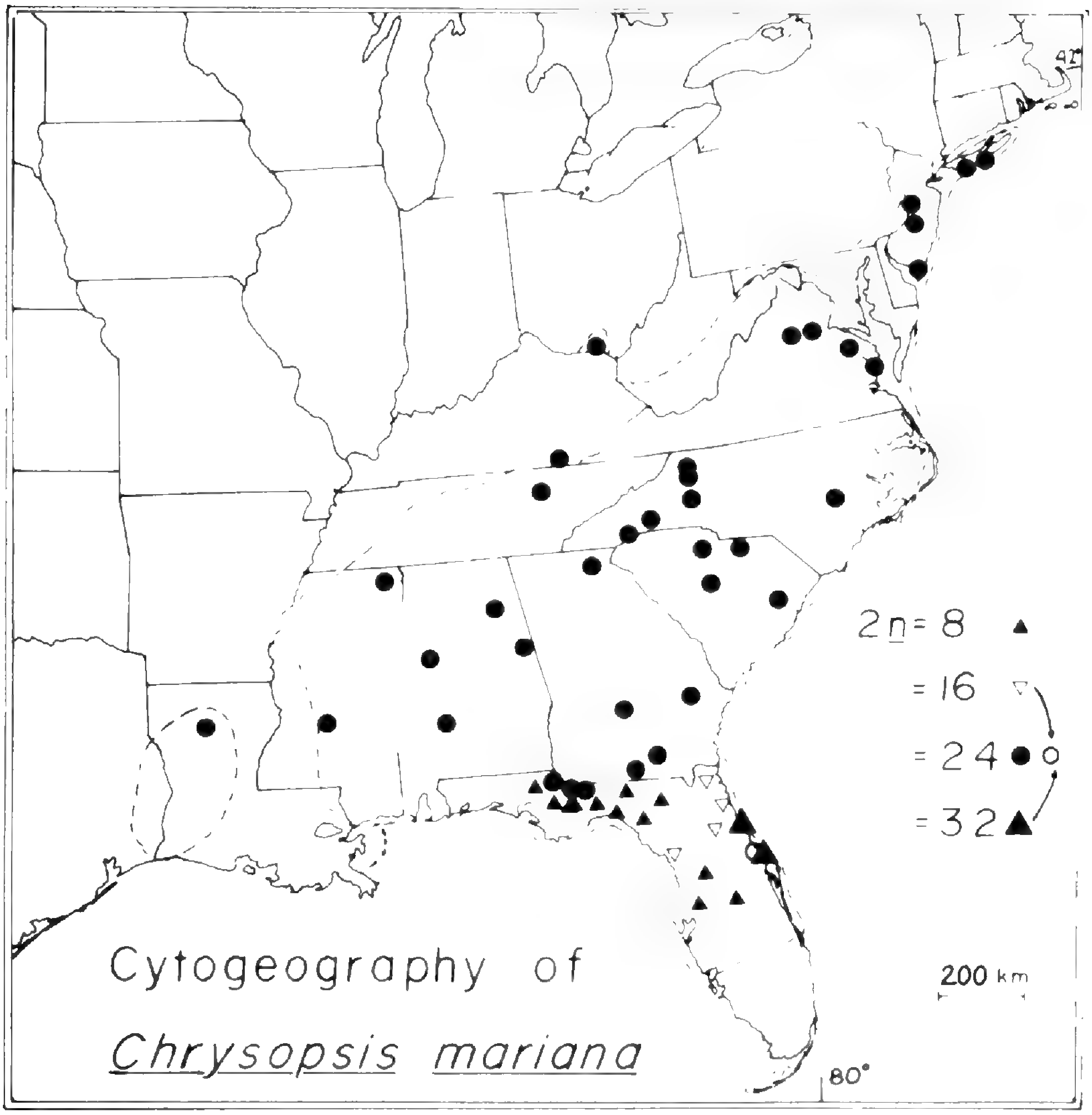

Figure 1. The cytogeography of *Chrysopsis mariana.* Superimposed on a state outline map of eastern United States are the range of the species (broken lines) and the locatons of all known populations from which chromosome numbers have been determined. A key to the symbols is included.

genus *Chrysopsis* (Semple, 1981). These same phenomena also appear to account for the pattern of cytotype distribution within *C. mariana.*

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J.C.S.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF WATERLOO
WATERLOO, ONTARIO N2L 3G1 CANADA

C.C.C.
DEPARTMENT OF BIOLOGY
UNIVERSITY OF CALGARY
CALGARY, ALBERTA T2N 1N4 CANADA

THE PRAIRIE FRINGED ORCHIDS: A POLLINATOR-ISOLATED SPECIES PAIR[1]

CHARLES J. SHEVIAK AND MARLIN L. BOWLES[2]

ABSTRACT

Plants referred in the past to *Platanthera leucophaea* (Nutt.) Lindl. have been found to comprise two species differing in pollination mechanisms, morphology, and geographic distribution. The more eastern species, *P. leucophaea,* is lectotypified, and the more western species is formally described as *P. praeclara.* Relationships of the species are discussed.

Key Words: Orchidaceae, *Platanthera leucophaea, Platanthera praeclara,* lectotype, pollination, evolution, biogeography

INTRODUCTION

The prairie fringed orchids, *Platanthera leucophaea* (Nutt.) Lindl. *auct.,* are some of the showiest plants in the genus. They are among only a few orchid species characteristic of the prairies of the central United States and are largely limited to this region. Although originally often frequent and occasionally occurring in vast numbers, they have become increasingly rare due to the wholesale destruction of the prairies. These circumstances have contributed to a great interest in these plants, yet they have been little studied and less understood. Their present rarity and characteristic drastic population fluctuations make them difficult subjects for observation.

Our familiarity with these plants is based on studies of their ecology (Sheviak, 1974; Bowles, 1983) and pollination biology (Bowles, unpub.). Examination of herbarium specimens suggested that plants from areas west of the Mississippi River were dramatically larger-flowered than more eastern plants, and the present study was initiated in order to assess the significance of this difference.

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[1] Published as New York State Museum Journal Series No. 438

[2] Present address: Natural Land Institute, 320 South Third Street, Rockford, Illinois 61108 and The Morton Arboretum, Lisle, Illinois 60532.

GARDEN AND FIELD STUDIES

A few plants from Illinois and Wisconsin had been cultivated by the authors for a number of years; others from North Dakota were collected for this study. In 1982 a plant from North Dakota and two from Wisconsin bloomed in cultivation at Albany and allowed comparison and experimentation. Forty-five populations also were studied in the field over a broad geographic area, including stations in North Dakota, Nebraska, Kansas, Minnesota, Iowa, Wisconsin, Illinois, Michigan, Ohio, and Ontario. These studies aided the assessment of the morphological differences noted in the cultivated plants.

Floral Characters

Under uniform light and temperature regimes, the first flowers on both the eastern and the western plants opened on the same day, suggesting no difference in phenology. The size differences apparent in herbarium specimens were evident also in live material (Figure 1), and floral characters including color, fragrance, shape of the lateral lobes of the lip, petal shape, and column structure also differed. The significance of most of these characters could not be judged from the small sample, but the differences suggested features for subsequent analysis. Differences in column structure, however, were of obvious significance, for the importance of column form in *Platanthera* speciation is well established (Stoutamire, 1974; Inoue, 1983).

Columns of the eastern plants were comparatively small and rounded. Pollinaria [hemipollinaria *sensu* Dressler, 1981] were closely spaced, the caudicles parallel, the viscidia directly below the pollinia, facing each other, and only 1.2–3.2 mm apart in the cultivated plants. In contrast, the larger columns of the western plant were noticeably angular, the caudicles widely diverging and directed somewhat forward, with the viscidia 6.2–7.5 mm apart. Field studies confirmed these differences in column structure and indicated that they are constant across broad geographic areas. It is apparent that the two column morphologies result in different pollinaria placement on pollinators and serve to isolate the plants through mechanics and pollinator specificity. Hence, the differences in column structure suggest that the eastern and western plants comprise different species.

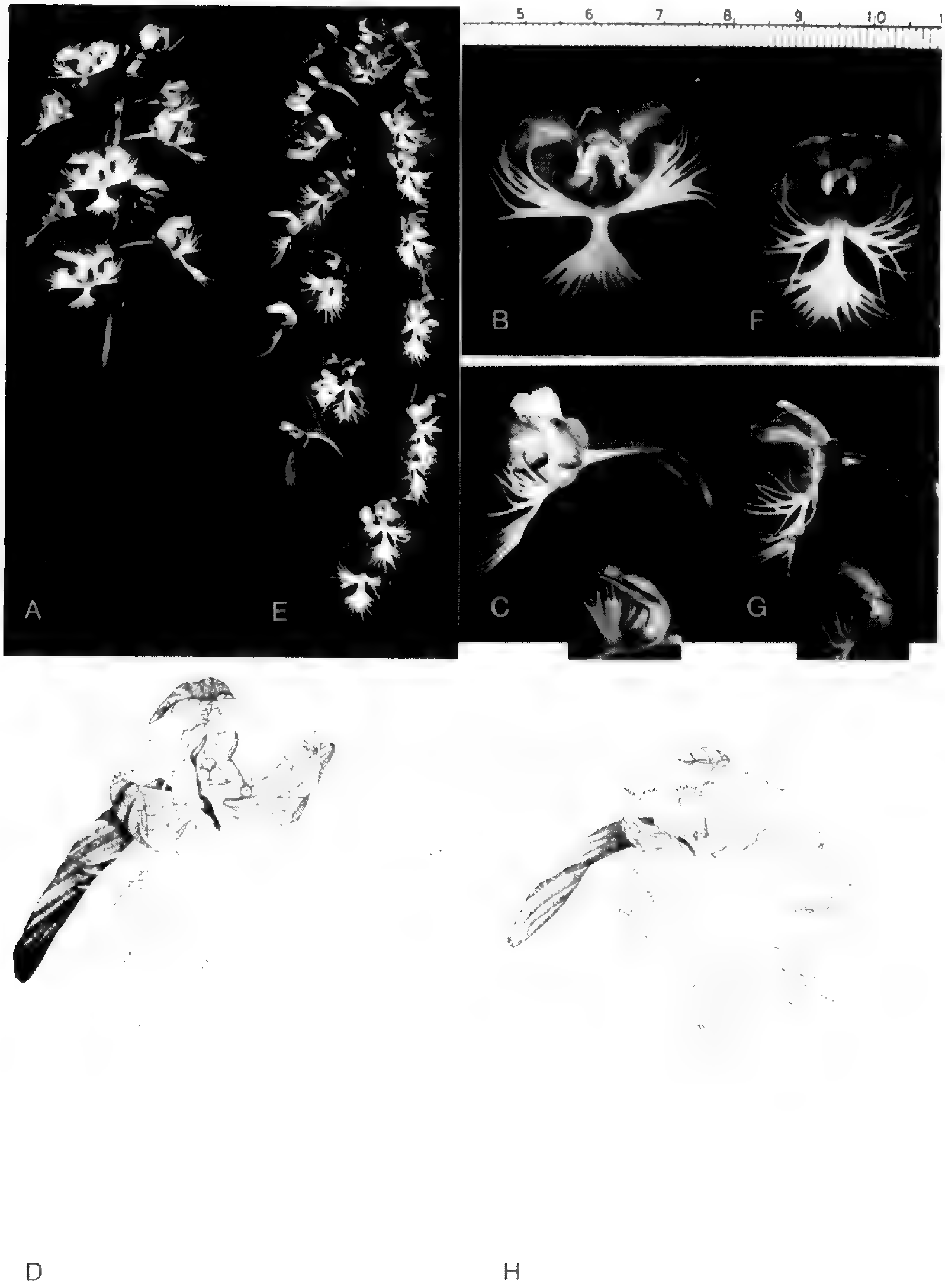

Figure 1. Inflorescences and flowers of *Platanthera praeclara* and *P. leucophaea.* **a–d**: *Platanthera praeclara.* **a–c**: *Sheviak 2222a,* Richland Co., North Dakota. **d:** *Bowles 501,* Ransom Co., North Dakota (isotype). **e–h**: *Platanthera leucophaea.* **e–g**: *Sheviak & Bowles 1828a,* Kenosha Co., Wisconsin. **h**: *Bowles s.n.,* Kenosha Co., Wisconsin.

Cytology

Chromosome numbers were determined for two cultivated plants each from North Dakota (*Sheviak 2222a, 2222b:* NYS) and Wisconsin (*Sheviak & Bowles 1828a, 1828b:* NYS). Mitotic figures were obtained from ovules and root tip meristems as in Sheviak and Catling (1980) and Sheviak (1982). All numbers were found to be $2n = 42$, and although this meager sample does not provide evidence on cytological conditions throughout the range of the plants, it does indicate that cytology is of no significance to the taxonomic problem at hand.

Hybridization

Cultivated plants blooming in 1982 were artificially hybridized and selfed to determine compatibility of eastern and western plants. Although limited, the results suggest compatibility. Copious seed resulted from all pollinations, and capsules appeared fully developed. Microscopic examination suggested that seed was comparable and highly fertile irrespective of parentage.

HERBARIUM STUDIES

Specimens were borrowed from herbaria located throughout the range of the plants. Virtually all specimens could be easily sorted on gross morphological differences into two groups of plants of comparatively eastern or western origin. Statistical analyses were then employed to determine which characters contributed to this ease of determination and to assess the variability and significance of the distinctive features noted in the live plants. Thirteen characters were measured on each of 29 eastern and 27 western specimens chosen to represent the evident range of variation in gross morphology and selected from across the plants' geographic ranges. Specimens chosen for measurement and their geographic origins are cited in Table 1. Characters measured and a summary of the measurements obtained is presented in Table 2. Most of these characters are self-explanatory, but a few require some discussion.

Spur maximum diameter measures the broadest part of the distal enlargement in the flattened state. Petal apex length is the length of the petal beyond its broadest point.

Column structure was severely distorted by pressing in all specimens examined, and after moistening with warm water, concentrated ammonia, strong saline, or other solutions, no clear indication of the original position of the viscidia was evident. Another character which might provide data related to viscidia orientation was consequently sought. In addition to a pronounced trend toward larger column size in the western plants, the shape of the columns when viewed from the side differs markedly (Figure 1). The rostellum lobes, which bear the caudicles and viscidia, are pronounced in the western plants, thrusting downward and forward in pressed material and providing the column with a strongly angular appearance. In eastern plants, the lobes are much smaller and give the column a more compact and rounded appearance. These differences·between columns of the two groups of plants are directly related to viscidia placement. Accordingly, a measurement was made of the height of the column from the apex of the lobe to the crown of the pollinium; this measurement most nearly assesses the key character of position of the viscidia.

Results of morphological analyses

Data derived from the 56 measured specimens were subjected to principal components analysis (SPSS: Factor). Two distinct groups were recognized by PCA (Figure 2), and these groups correspond to the eastern and western groups which had been established by subjective consideration of gross morphology. This correlation extends even to a few atypical or seemingly out-of-range specimens which had been determined by consideration of a combination of characters stressing column morphology. The PCA results support these determinations and further indicate the validity of the eastern and western concepts.

Utilizing the groupings established by subjective study and PCA, a stepwise discriminant function analysis (SPSS: Discriminant) was performed in an effort to determine the significance of individual characters and to aid in determination of herbarium material (Figure 3 and Table 2). Again, in DFA two groups are clearly established, and these groups correspond to those obtained by subjective determination and by PCA. Significant characters for determination were, in order of decreasing importance: lateral sepal width, column height, inflorescence length, spur length, lateral sepal length, and flower number. These results establish the utility of column height as a character and also identify several other characters that clearly contribute to subjective determination.

Table 1. Specimens of *Platanthera leucophaea* and *P. praeclara* employed in statistical analyses by subjectively determined group.

Locality [County]	Specimen
Eastern (*P. leucophaea*)	
ONTARIO	
Huron	*Morton s.n.* (DAO 328245b)
Middlesex	*Burgess 1769* (DAO)
Simcoe	*Walshe 143* (DAO)
NEW YORK	
Oswego	*Wibbe s.n.* (NYS)
Wayne	*Hankenson s.n. "a"* (NYS)
NEW JERSEY	
Sussex	*Rushby s.n.* (F349473)
OHIO	
Stark	*Reihl s.n.* 7/1835 (MO)
MICHIGAN	
Cheboygan	*Erlanson 481c* (MICH)
Cheboygan	*Ehlers 2507a* (NYS)
Eaton	w/o collector (NYS)
Tuscola	*Case s.n.* 7/14/61 (MICH)
INDIANA	
Elkhart	*Deam 57927* (IND)
Hamilton	*Shipman 2765* (MICH)
Lagrange	*Deam 20669* (IND)
Laporte	*Deam 55231b* (IND)
WISCONSIN	
Jefferson	*Wadmond 1504* (MINN)
ILLINOIS	
Cook	*A. Chase 1381a* (ILL)
Cook	*McDonald s.n.* 6/1886 (ILL)
Cook	*Hill 58, 1875b* (ILL)
Cook	*Babcock s.n.* (F33398)
Fayette	*Benjamin s.n.* 6/14/1948 (ILL)
Kankakee	*Hill 231, 1873* (ILL)
Madison (?)	*Eggert s.n.* [*ex* Denslow 142] (NYS)
McDonough	*Young s.n.* (IND)
McDonough	*Myers 632* (MWI)
Stark	*V. Chase 665* (ILL)
Winnebago	*Bebb s.n.* (F62188)
IOWA	
Henry	*Mills 1843* (MO)

NEBRASKA	
Dodge	*Engberg s.n.* (NEB169756)
Western (*P. praeclara*)	
MINNESOTA	
Clay	*Ottoson 98* (MINN)
Faribault	*Shimek s.n.* (NEB59440)
Fillmore	*Hill s.n.* "*a*" 7, 1861 (ILL)
Freeborn	*Rosendahl et al. 7277* (MINN)
Houston	*Wheeler 299* (MINN)
Kandiyohi	*Frost 316* (MINN)
Nicollet	*Ballard 1067* (MINN)
Polk	*Ownbey 4954a* (MINN)
IOWA	
Black Hawk	*Burk 601* (ILL)
Decatur	*Fitzpatrick & Fitzpatrick 18* (MO)
Dickinson	*Shimek s.n.* (F1564537)
Emmet	*Cratty s.n.* (NYS)
Pottawattamie	*Shimek s.n.* (MO1245647b)
Union	*Fay 3156* (TEX)
Webster	*Churchill 1110a* (NEB)
Webster	*Churchill 1110b* (NEB)
Winneshiek	*Tolstead s.n.* (NEB236617)
NORTH DAKOTA	
Ransom	*Seiler 3460* (MO)
Richland	*Seiler 3344* (KANU)
SOUTH DAKOTA	
Minnehaha	*Over 7030* (SDU)
NEBRASKA	
Cass	*Fricke s.n.* (NEB169784)
Chemung	*Devorak s.n.* (NEB169781)
Cherry	*Smith & Pound 219a* (NEB)
Dodge	*Eastman s.n.* (NEB169755a)
Grant	*Bates s.n.* (NEB169786)
Otoe	*Turrell s.n.* (NEB242215)
KANSAS	
Douglas	*Snow 8061* (KANU)

Table 2. Means, standard deviations, and discriminant function character weights for the 56 specimens of *Platanthera* cited in Table 1.

Character	Means (σ)				Discriminant Function Character Weights*
	East [*leucophaea*]		West [*praeclara*]		
Column height	3.9	(0.4)	6.5	(0.8)	1.04734
Lateral sepal					
length	8.1	(1.2)	12.0	(1.1)	.24089
width	5.0	(0.6)	8.3	(1.0)	.51681
Lip					
length	18.0	(2.3)	25.6	(3.4)	
width	20.5	(2.9)	30.0	(5.0)	
Spur					
length	35.6	(4.8)	45.7	(5.9)	.08228
maximum diameter	1.8	(0.3)	2.7	(0.5)	
Petal					
length	9.6	(1.3)	13.1	(1.8)	
width	5.8	(1.2)	9.5	(1.9)	
apex length	2.6	(0.6)	2.7	(0.6)	
Flower number	19.4	(7.9)	12.6	(4.5)	.07686
Inflorescence length	122.7	(48.2)	92.1	(32.3)	−.02894
Plant height	676.4	(191.0)	566.3	(138.2)	

*From the sum of the products subtract the constant 12.61585.

The significance of the correlation between morphological groups and column structure is clear: the eastern and western plants represent distinct species.

TYPIFICATION OF *Platanthera leucophaea*

Orchis leucophaea Nutt., a product of Nuttall's 1819 collecting in the Arkansas Territory, was described from "Kiamesha, Red River" (Nuttall, 1834). For several days in June of that year, he collected on calcareous prairies in the vicinity of the confluence of the Kiamichi and Red Rivers, in the present state of Oklahoma (Nuttall, 1821). This site is south of the known range of the western species and is far disjunct from that of the eastern. The apparent type collection comprises two sheets, one each at PH and BM. The sheet at PH bears Nuttall's original field label with the characteristically cryptic notation ""Fl. O * (Nutt.) Ark. Red riv."" This specimen is an inflores-

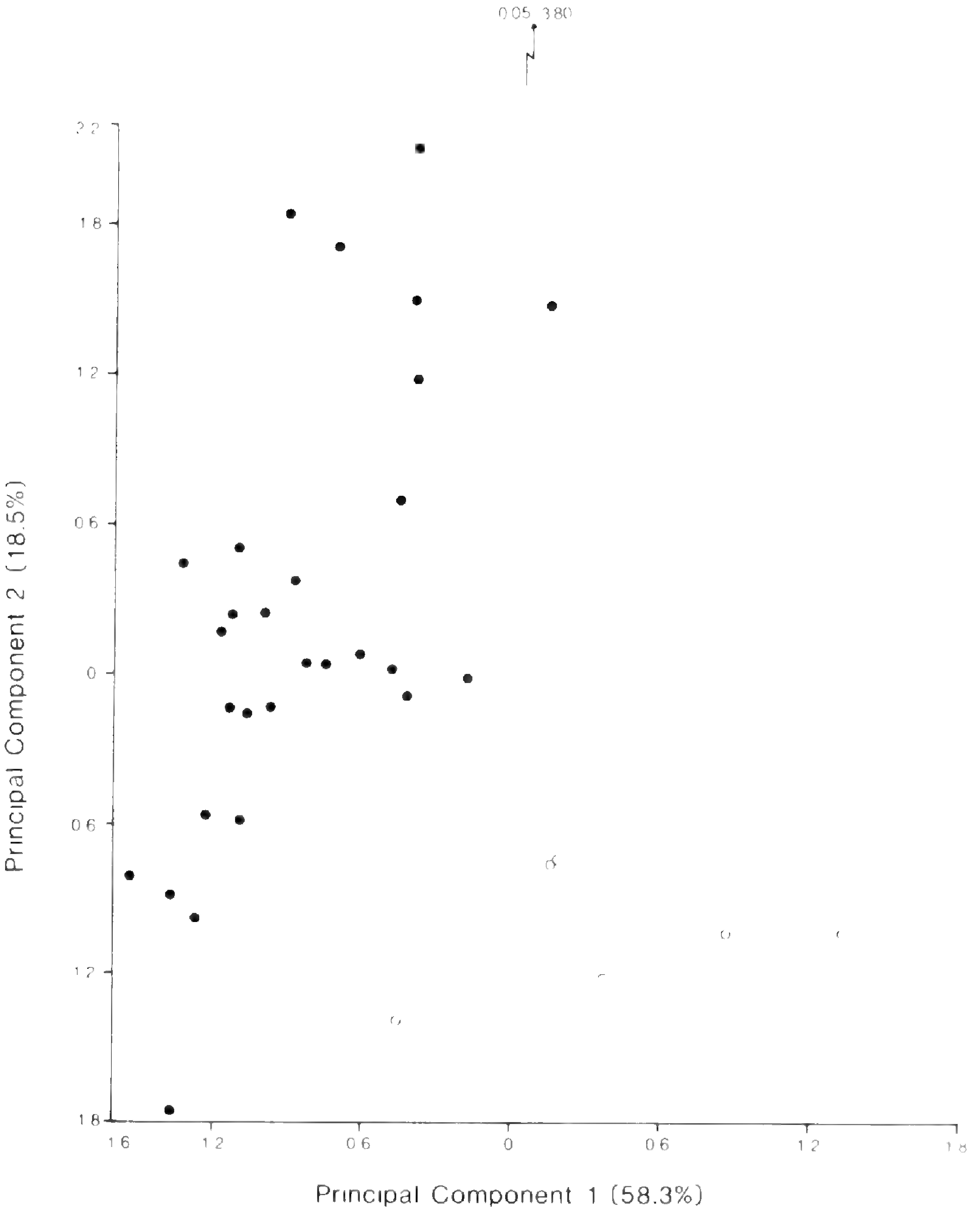

Figure 2. Positions of 56 specimens on the first and second principal components derived from measurements of 13 morphological characters in moistened herbarium specimens. Solid dots – *P. praeclara*; open circles = *P. leucophaea.*

cence which, after pressing, was nearly destroyed by insects. The sheet at BM bears a more carefully executed label, on which is written, apparently in the same hand, "Orchis *leucophaea Red River Prairies," with "leucophaea" crossed out. On this sheet are mounted two specimens, one a leafy stem with an inflorescence very similar to that of the PH specimen and also heavily damaged by

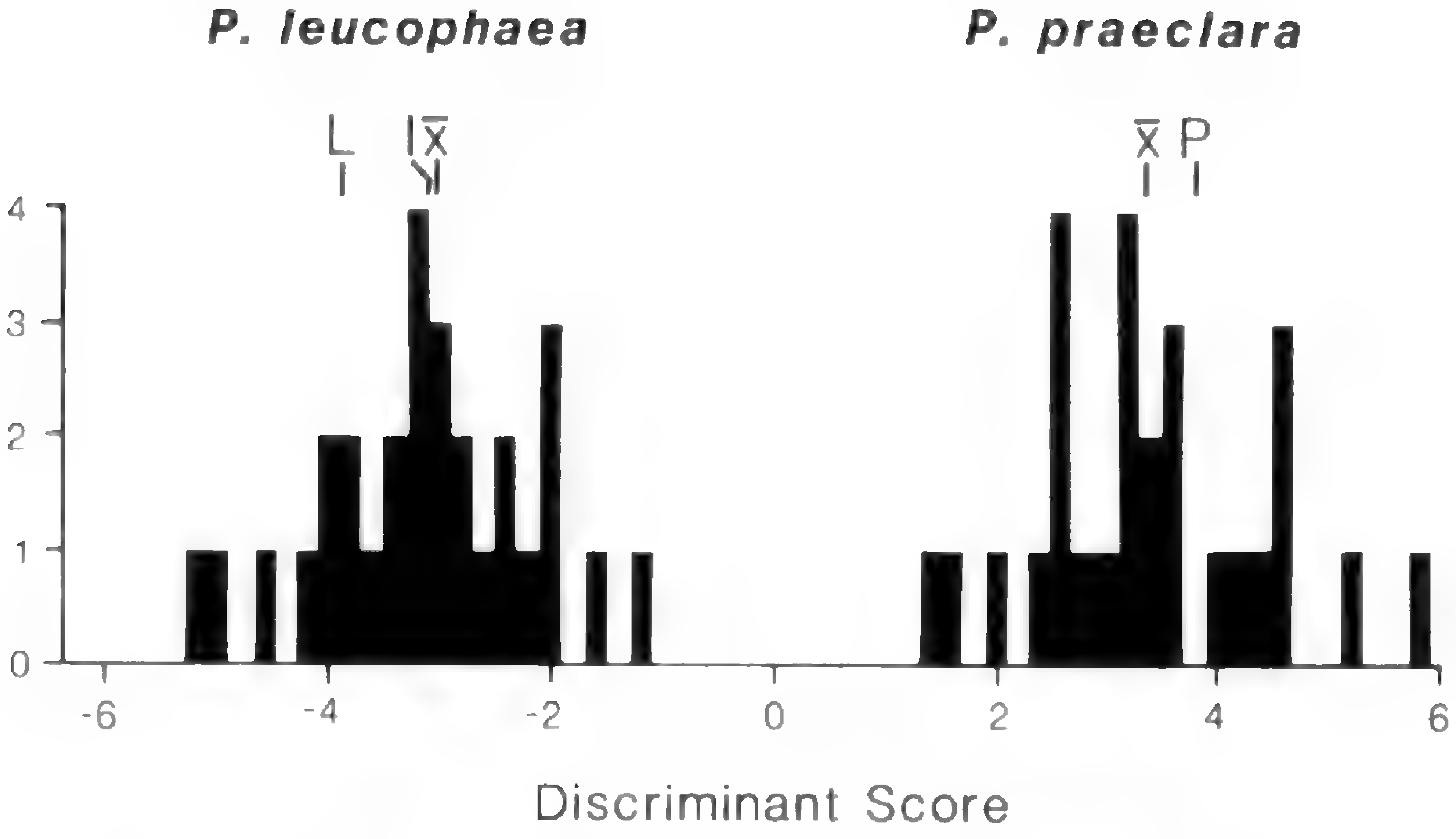

Figure 3. Histogram of discriminant scores of 27 specimens of *Platanthera praeclara* and 29 of *P. leucophaea*. Also plotted are group centroids ($\bar{x}$), the holotype of *P. praeclara* (P), a topotype of *P. leucophaea* [*Leavenworth s.n.*, NY] (I), and the lectotype of *P. leucophaea* (L). Measurements of the lectotype were made on dry flowers and then adjusted for the projected effects of moistening, based on the actual changes in each measurement in the topotype. An estimate of two additional flowers was included to compensate for a missing segment of the rachis. Failure to adjust for dry material and for missing flowers each shifts the score to more negative values.

insects, and the other an inflorescence of *P. grandiflora* (Bigel.) Lindl. with a number of flowers in excellent condition. The identity of this second inflorescence and lack of insect damage to it indicate a mixture of collections in the herbarium; this mixture may have led to the name having been crossed off the label. The more complete BM specimen and the specimen at PH, despite their poor condition, are readily identifiable and are clearly of the eastern species. This identity and the inclusion of the inflorescence of *P. grandiflora* raise the question of authenticity of the specimens. Are these the specimens Nuttall collected at the type locality, or might they be others with which he replaced a missing type? Nuttall is known to have lost and replaced other specimens (Stuckey, 1967). A few years after Nuttall's publication, the eastern plant was collected in Ohio by Sullivant; his plants were subsequently cultivated at the Cambridge (Massachusetts) Botanic Garden, which Nuttall curated until 1834. Perhaps Nuttall collected the specimens on a later visit to the garden. In order to assess this possibility, an effort was made to locate any duplicate of the type which Nuttall might have sent to Hooker, de Candolle, or other correspondents. Nuttall apparently did not distribute duplicates of his new Arkansas species, however (Graustein, 1967), and, indeed, none has been located. Less direct means of establishing the authenticity of the specimens were consequently necessary.

Documentation of the presence of the eastern species in southern Oklahoma is provided by two collections at PH and NY. One specimen, from the Short herbarium at PH, is labelled "Flowering in June, vicinity of Fort Towson" (written) and "Dr. Leavenworth, Fort-Towson, Arkansas" (printed). Unfortunately, a note on the sheet indicates that the label may have been interchanged with a Sullivant specimen from Ohio. Both of the specimens involved are clearly of the eastern species, but the possibility of confusion prevents the unequivocal establishment of the identity of the plant at the collection site. The second specimen is then useful for verification. A part of the Torrey Herbarium at NY, it is labeled simply "Arkansas, Dr. Leavenworth, 1837." An army surgeon, M. C. Leavenworth was stationed for five years in western Louisiana and southeastern Oklahoma. During the growing seasons of 1834 and 1835, he was stationed along the Red River, Arkansas Territory, first in the Cross Timbers region and later at Fort Towson. Late in 1835 he was transferred to Florida and was forced to leave extensive botanical collections at the fort. In 1836, he was transferred to Fort Jessup, Louisiana (where he had been stationed prior to his assignment in Arkansas Territory) and later to Camp Sabine. During his years in Louisiana he collected in that state and in Texas, and he is not known to have collected again in the Arkansas Territory (McVaugh, 1947). He began in 1836 to ship specimens to Torrey, and the date on the specimen evidently records the year in which Torrey received it. Leavenworth received a shipment of his Arkansas specimens while at Camp Sabine (letter to Torrey, 22 Jan 1837) and later that year expressed his pleasure at Torrey's receipt of unspecified Arkansas specimens (letter to Torrey, 1 Jul 1837). From what is known of Leavenworth's travels, it is evident that the specimen was collected along the Red River in southeastern Oklahoma, and it is reasonable to conclude that both specimens are from the same locality. Fort Towson was located near the mouth of the Kiamichi River, and hence Leavenworth's specimens are evidently topotypes; they clearly establish the presence of the eastern plant along the Red River.

The Leavenworth specimens indicate that Nuttall could indeed have collected the eastern species in Oklahoma. The specimen at PH and the more nearly complete of the two at BM are parts of the type collection, and the name *Orchis leucophaea* is properly applied to the eastern species. The flowers of the PH specimen collectively display all floral features; this is not the case on the specimen at BM. This situation, together with slightly better data on the original field label at PH and the mixture at BM, leads us to designate the specimen at PH as lectotype. The western species is described here:

Platanthera praeclara Sheviak & Bowles, *sp. nov.* (Figures 1a–d; 4)

Flores maximi, eburnei, albescentes. Sepala ovata vel suborbiculata, 9.0–14.1 mm longa, 6.8–10.0 mm lata. Petala flabellata, truncata, saepe emarginata, 9.0–16.5 mm longa, 6.5–13.5 mm lata. Labellum 17–32 mm longum, 20–39 mm latum, penitus trilobum, lobis flabellatis, incisis, fimbriatis. Calcar gracile, clavulatum, 36–55 mm longum. Columna lata, rostello bilobo, lobis triangularibus, patentibus, viscidiis 6–7 mm disjunctis.

Herb erect, stout, 38–85 cm tall, glabrous throughout. Leaves lanceolate to ovate-lanceolate, ascending, the bases sheathing the stem, up to 26 cm long, 5 cm wide. Raceme large, showy, 4.8–11.6 cm long, 5.5–9.0 cm wide. Flowers creamy white, very large. Ovaries slender, up to 27 mm long. Sepals ovate to suborbicular, the lateral obliquely asymmetrical, 9.0–14.1 mm long, 6.8–10.0 mm wide. Petals flabelliform, truncate, often emarginate, the apical margin lacerate, 9.0–16.5 mm long, 6.5–13.5 mm wide. Lip deeply three-lobed, the lobes narrowly to broadly flabellate, the lateral sometimes very broad and overlapping the median, deeply incised and fringed, 17–32 mm long, 20–39 mm wide. Spur slender, curving, clavellate, 36–55 mm long. Column broad, the rostellum two-lobed, the lobes triangular, wide-spreading, the viscidia 6–7 mm apart. Chromosome number $2n = 42$.

TYPE: U.S.A. North Dakota. Ransom Co.: Swales in sand prairie haymeadows being mowed for hay. Sheyenne National Grasslands, T134N, R53W, Fifth Principal Meridian. 14 July 1982. *M. L. Bowles 501* (HOLOTYPE: NYS; ISOTYPE: AMES, F, ILL, NY).

Etymology: The epithet *praeclara* was chosen for its singularly appropriate series of translations: very bright, beautiful, splendid, glorious, distinguished, noble.

COMPARATIVE MORPHOLOGY

Platanthera praeclara is very similar to *P. leucophaea* in gross morphology, but the two species are readily separated by a number of floral characters. Most of these directly reflect the larger size of the flowers of the former species, and these differences are apparent in Figure 1 and Table 2. Other characters include flower color, fragrance, lip and petal shape, sepal shape, flower number, and the length and density of the inflorescence. The salient character, column structure, has been treated in the discussions of garden and herbarium studies and is well depicted in Figure 1.

Floral color tends to differ slightly. The lip and petals of *Platanthera praeclara* are predominantly a creamy white, and the sepals are similar although suffused with a faint greenish cast. In contrast, flowers of *P. leucophaea* appear markedly whiter due to the lip and petals being pure white and contrasting strongly with their green claws and wholly green sepals. Flowers of *P. praeclara* often fade to white as they age, however, and the sepals of *P. leucophaea* may be somewhat whitish.

Floral fragrance in both *Platanthera praeclara* and *P. leucophaea* is light and very sweet, and intensifies after sunset. In the cultivated plants, however, the fragrance of *P. leucophaea* is somewhat more spicy than the very delicate scent of *P. praeclara*. This difference is quite apparent and was noted by other observers.

The obvious difference in the shape of the lateral lobes of the lip in the cultivated plants (Figure 1) is not taxonomically significant. The broad, downward-spreading lobes of the *Platanthera leucophaea* flower and the much narrower lobes in *P. praeclara* are representative of the species, but variation is common.

Petal shape tends to differ markedly between the species. The petals of *Platanthera praeclara* are nearly triangular in outline, very broad, truncate, and often somewhat emarginate. Those of *P. leucophaea*, in contrast, are typically merely obovate, but occasionally vary toward those of *P. praeclara*.

The sepals of *Platanthera praeclara* are comparatively broader than those of *P. leucophaea*. The importance of lateral sepal size (as determined by DFA), in contrast to various corolla characters is perhaps surprising, but is easily understood. Sepal enlargement is negligible after the flower opens, whereas the petals and lip greatly increase in size. Hence corolla measurements will vary depending on age of the flower, and their maximum dimensions might be environmentally influenced. The differences in bud size (reflected in sepal measurements) contribute significantly to the different aspects of the plants.

Flower number, inflorescence length, and apparent density of the inflorescence are related characters which contribute to the distinctive aspects of the two species. Flowers are generally fewer and the inflorescence shorter in *Platanthera praeclara* than in *P. leucophaea*. Because of the larger flower size in *P. praeclara*, spaces between flowers are much reduced and the inflorescence typically appears much more dense than in *P. leucophaea*. In general, *P. praeclara* produces shorter, denser inflorescences of fewer, larger buds and flowers than *P. leucophaea*.

ECOLOGY

The ecology of these plants has been discussed by Bowles (1983). West of the Mississippi River and in much of the prairie peninsula, *Platanthera leucophaea* and *P. praeclara* occupy mesic to wet calcareous prairie. Further eastward, however, *P. leucophaea* occurs in a region supporting a much more diverse assortment of habitats, and it also occurs in marshes, fens, and bogs. These plants exhibit adaptations to periodic drought and may exist in a subterranean, dormant or mycotrophic state for one or more years; they are noted for dramatic, periodic mass flowerings following several-year periods of apparent absence. This behavior appears to be linked to fire-stimulated growth and flowering, although other factors, such as rainfall and soil moisture levels, are likely involved as well.

POLLINATION BIOLOGY

These plants are classic examples of phalaenophily (Faegri and van der Pijl, 1971) and, more specifically, sphingophily (van der Pijl and Dodson, 1966). The horizontally displayed flowers are nocturnally fragrant, white, without colored nectar guides, deeply fringed, bilaterally symmetrical, with extruded columns, and with nectariferous spurs that are the longest of any north temperate member of the genus. Within this general syndrome, column structures of *Platanthera leucophaea* and *P. praeclara* dictate different pollination mechanisms. The restricted spur entrance controls pollinator position in the "key-hole" sense of Dressler (1981), and pollinaria placement is limited to either the proboscis or eyes, which are the only organs to which the viscidia will adhere properly.

Sphingophily in *Platanthera leucophaea* is supported by Robertson (1893), Case (1964), and our observations. [Moth specimens to be deposited at Entomology Laboratory, University of Wisconsin, Madison.] Robertson is the only worker to have identified pollen vectors [*Xylophanes tersa* (L.) and *Eumorpha achemon* (Drury): Sphingidae] and to have described pollination mechanics. He reported that pollinaria were deposited on the proboscis and usually were removed one at a time, as the viscidia were only 2 mm apart and the moth directed its proboscis to one side or the other. From this information it is clear that his observations pertain to *P. leucophaea*. Pollination in *P. praeclara* has not been reported.

Pollination of *Platanthera leucophaea* and *P. praeclara* was studied in the field from 1979 to 1983. Even when working with ultraviolet lights and red-filtered lanterns, observation of swift-flying nocturnal pollinators is difficult, and only three visitations by sphinx moths have been witnessed. At *P. leucophaea, Sphinx eremitis* (Hübner) was collected while feeding at flowers and was found to carry a pollinarium at the base of its proboscis; *Manduca sexta* (L.) was observed and photographed while feeding but was not collected. In both cases abundant seed set occurred, and these insects probably were pollinators. *Manduca quinquemaculata* (Haw.) was collected while visiting *P. praeclara,* but pollinaria removal was not evident, and the insect probably was not a pollinator.

In order to gain more information, pollination was studied under controlled conditions in Rockford using potted *Platanthera leucophaea* and *P. praeclara* and laboratory-reared *Manduca sexta*. These long-tongued moths (see below) served as pollinators of *P. leucophaea,* contacting viscidia and removing pollinaria with the proboscis. Most moths were able to reach nectar of *P. praeclara* without effecting pollination, but one individual with an abnormally short proboscis contacted viscidia and removed pollinaria with its eyes.

Following removal of pollinaria, the caudicle taxis necessary to orient the pollinia for stigmatic contact on subsequent visits is markedly different in the two species. Pollinaria of *Platanthera leucophaea*, initially born vertically, bend forward, assuming a position nearly parallel to the proboscis, and with the pollinia only slightly elevated. This position is necessary in order for them to be inserted between the closely-spaced rostellum lobes and to contact the recessed stigma. In contrast, pollinaria of *P. praeclara* rotate laterally, either toward the left or right, assuming a central position above and slightly forward of the moth's head. This position permits contact with the stigma without interference from the wide-spread rostellum lobes.

These different movements and column structures provide a physical barrier to hybridization between *Platanthera leucophaea* and *P. praeclara*. A laterally oriented pollinarium of *P. praeclara* borne on a moth's eye will be deflected by the rostellum lobes of *P. leucophaea* and will not contact the deeply recessed stigma. Forward-directed pollinia of *P. leucophaea* will be unaffected by the wide-spread rostellum lobes of *P. praeclara*, but the larger flower dimensions of the latter species suggest that the position of the pollinia close to the proboscis may prevent their contacting the stigma elevated above the entrance to the spur. Hence, hybridization between *P. leucophaea* and *P. praeclara* would appear to be unlikely, even in mixed populations.

The different pollination mechanics of *Platanthera leucophaea* and *P. praeclara* reflect selection for different groups of pollinators. Placement of pollinaria on eyes dictates a certain pollinator specificity, for spur length and the distance between the viscidia together limit pollinator dimensions. Proboscis length must be sufficient to reach nectar, but not so great as to prevent the moth's eyes from contacting the viscidia, and the distance across the eyes must approximate that between the viscidia. Longer-tongued moths will be able to reach nectar without contacting the viscidia, and moths with a small distance across the eyes will not remove pollen regardless of proboscis length. Measurement of spurs in herbarium specimens of *P. praeclara* (Table 2) disclosed a mean length of 45.7 mm ($\sigma = 5.9$). The volume of nectar in unvisited flowers appears to vary greatly, but data could not be obtained from unbagged specimens in the field. Field experience and study of the plant in cultivation suggest that the distal 10–15 mm of the spur are commonly filled with nectar. Assuming 10 mm as an average minimum, maximum proboscis lengths of primary pollen vectors would need to occur within an extreme range of 30–50 mm, and more likely 35–45 mm. Moths with proboscis lengths greater than spur length, and moths with the distance across the eyes much less than the distance between the viscidia will not serve as pollinators and will function as nectar thieves.

Proboscis lengths in prairie region sphinx species vary greatly. Gregory (1964) and Fleming (1970) listed values for several species. During the present study, measurements were made of one or two specimens [NYSM] each of nineteen common prairie region species. Of these, five had reduced, non-functioning mouth parts [*Pachysphinx modesta* (Harr.), *Paonias excaecatus* (J. E. Smith), *P. myops* (J. E. Smith), *Smerinthus cerisyi* Kby., *S. jamaicensis* (Drury)]; in nine, the proboscis was too short to reach the nectar in most flowers [10–20 mm: *Amphion floridensis* B. P. Clark, *Ceratomia amyntor* (Geyer), *C. undulosa* (Wlk.), *Darapsa myron* (Cram.), *D. pholus* (Cram.), *Deidamia inscripta* (Harr.), *Hemaris diffinis* (Bdv.); 21–25 mm: *Hemaris thysbe* (F.), *Sphinx gordius* Cram.]; and five had proboscis lengths sufficient to reach common nectar levels [34–43 mm: *Eumorpha achemon* (Drury), *Hyles lineata* (F.), *Sphinx drupiferarum* J. E. Smith, *S. kalmiae* J. E. Smith, *S. vashti* Stkr.]. Significantly, in this last group the measurements across the eyes of all but *S. vashti* were highly consistent, 5.8–6.4 mm, figures closely corresponding to viscidia separation in *Platanthera praeclara*. Hence, these species could serve as pollinators. In contrast, this measurement varied greatly (3.7–6.2 mm) in the shorter-tongued species and was not correlated with proboscis length. In *S. vashti*, with a proboscis length of 34 mm, the distance across the eyes was only 4.7 mm, suggesting that the moth might often fail to contact viscidia, despite its moderate proboscis length. Consequently, this species may serve as a nectar thief. In *Manduca quinquemaculata* and *M. sexta*, proboscis lengths average 80 to 130 mm (Gregory, 1964; Fleming, 1970), and these species are very likely nectar thieves, a conclusion supported by our pollination experiments. Gregory's report of a mean of 60 mm for *Sphinx drupiferarum* suggests that this species may also at times function as a nectar thief, although his more western populations may not be representative of moths from the prairies.

Flowers of *Platanthera leucophaea*, in contrast, deposit pollinaria on the proboscis at precisely the correct point for later stigmatic contact. Hence a wide range of proboscis lengths is acceptable, and eye relationships are irrelevant. Nectar production in these plants is highly variable (Bowles, unpubl.). The distal 10–15 mm of the spur is dilated and accumulates a larger quantity of nectar than the more slender tube. Assuming 15 mm as a common maximum, the mean spur length of 35.6 mm ($\sigma = 4.8$) in these plants (Table 2) suggests that a minimum pollinator proboscis length of 15.8 mm has been selected for in this species. Some spurs of unvisited flowers, however, over time may become entirely nectar-filled, and shorter-tongued moths may then obtain nectar. It may be significant that flowers of *P. leucophaea* are occasionally visited by noctuids and other moths. These species may remove pollinaria, and although short-tongued and inefficient at nectar removal, they routinely visit a number of flowers and may function at least as secondary vectors.

Our field observations of *Manduca* in natural populations of *Platanthera leucophaea* and *P. praeclara* support an hypothesis of nectar thievery. In one population of *P. praeclara* (Adair Co., Iowa), most inflorescences showed signs of visitation (low nectar levels), yet few pollinaria were removed and a specimen of *Manduca quinquemaculata* captured while visiting the plants bore no pollinaria. A population of *P. leucophaea* (Grundy Co., Illinois) at which *Manduca sexta* was observed and photographed (but not collected) had a high frequency of pollinaria removal.

RELATIONSHIPS

Platanthera praeclara and *P. leucophaea* form a species pair closely related to another evident pair, *P. grandiflora* (Bigel.) Lindl.–*P. psycodes* (L.) Lindl., and to two other species, *P. peramoena* (A. Gray) A. Gray, and *P. lacera* (Michx.) G. Don. These six species form a natural group. Their relationships have been interpreted by Stoutamire (1974), who stressed column structure and resulting differences in placement of pollinaria on pollinators. He proposed two evolutionary lines, one marked by eye-deposited pollinaria (*P. grandiflora, P. peramoena*) and the other by deposition on the proboscis (*P. psycodes, P. lacera*). He suggested that the great similarity in gross morphology between *P. grandiflora* and *P. psycodes* was not due to a close relationship but rather to convergent specialization for diurnal lepidopteran pollination. This conclusion was supported by hybridization data which suggested that *P. grandiflora* was somewhat isolated from *P. psycodes* and *P. lacera* but that these latter two species hybridized successfully and were apparently isolated primarily by pollinator differences. His understanding of the prairie species was incomplete, but from his description of the column it is clear that his comments refer to *P. leucophaea.* He considered its column to be somewhat intermediate between the two primary types, and he suggested that *P. leucophaea* arose from the *grandiflora-peramoena* line through specialization for sphinx pollination.

The recognition of a sphinx-pollinated species pair comparable to the *grandiflora-psycodes* pair suggests that pollination mechanism and attendant column structure may not indicate evolutionary lines in the group, but rather may have been repeatedly selected in response to similar pressures. This interpretation is based on the evidently close relationship between *Platanthera leucophaea* and *P. praeclara,* a relationship apparent from similarities in morphology and, perhaps, habitat preferences. Although the species are strikingly similar and, together, dramatically different from their relatives, most of the obvious differences reflect specialization for sphingophily and could be the result of convergence. Other floral features not obviously part of the syndrome, however, also suggest a relationship. These include the triangular petals of *P. praeclara* and some *P. leucophaea;* the broad, downward-spreading lateral lobes of the lip in *P. leucophaea* and some *P. praeclara;* and the orientation of the pollinia, which in these species are directed forward, forming a hood at the apex of the column. These features represent extreme developments of tendencies present in the other species of the group; their coincident expression in these very similar species indicates a close relationship. This relationship is also reflected in vegetative habit, a character which also discriminates the *psycodes-grandiflora* pair. Each of these pairs represents opposite extremes in the pattern of vegetative variation in the group. Leaves of *P. leucophaea* and *P. praeclara* are comparatively short, broadest near the base and tapering to acute apices, rigidly ascending with the broad bases prominently infolding and sheathing the stem. In *P. psycodes* and *P. grandiflora,* leaves are longer, broadest near or above the middle and rounded to a blunt apex, and wide-spreading to drooping. Hence, the species pairs are evident also from vegetative features.

Viscidia provide additional evidence of significance to evolutionary interpretation. In *Platanthera*, viscidia highly specialized for proboscis deposition are elongated, whereas those deposited on eyes are round (Inoue, 1983). Viscidia in *P. lacera* are linear-oblong, and those in *P. grandiflora* and *P. praeclara* are round. Those of *P. leucophaea*, however, are very similar to those of *P. praeclara*, and in *P. psycodes* they are narrowed only slightly and are rather variably shaped, but definitely not elongated. This situation suggests that *P. leucophaea* and *P. psycodes* are less completely adapted to proboscis deposition than is *P. lacera*, and that these three species do not form an evolutionary line. Stoutamire's hybridization data do not provide unequivocal evidence on relationships, because the indicated isolation may either initiate or result from speciation; furthermore, our data suggest compatibility between *P. praeclara* and *P. leucophaea*. Consequently, it appears unlikely that the coincident patterns of floral and vegetative characteristics evident in the two species pairs are the results of repeated selective events. It is more reasonable to view the two white-flowered species and the two purple-flowered species as two pairs of closely related species, with the members of each pair isolated by differences in pollination mechanics. In each case it seems most likely that the proboscis-depositing column type arose from the other type as an adaptation reducing nectar thievery and increasing reproductive efficiency. This hypothesis is supported by the biogeography of the species.

BIOGEOGRAPHY

Platanthera leucophaea and *P. praeclara* are essentially allopatric (Figure 4). The western *P. praeclara* occupies an area largely corresponding to the Missouri River drainage, the center of the tallgrass prairie formation. In contrast, *P. leucophaea* occurs primarily in the upper Mississippi River drainage and the Great Lakes region in an area corresponding to the prairie peninsula. From this region, disjunct stations are scattered eastward through a zone rich in prairie species. The Red River occurrences probably represent relictual populations.

The prairie peninsula is a comparatively young feature which appears to have developed in a northeastward direction following the close of the Wisconsinan glaciation. Since then, its eastern margins have been retreating westward, leaving behind numerous

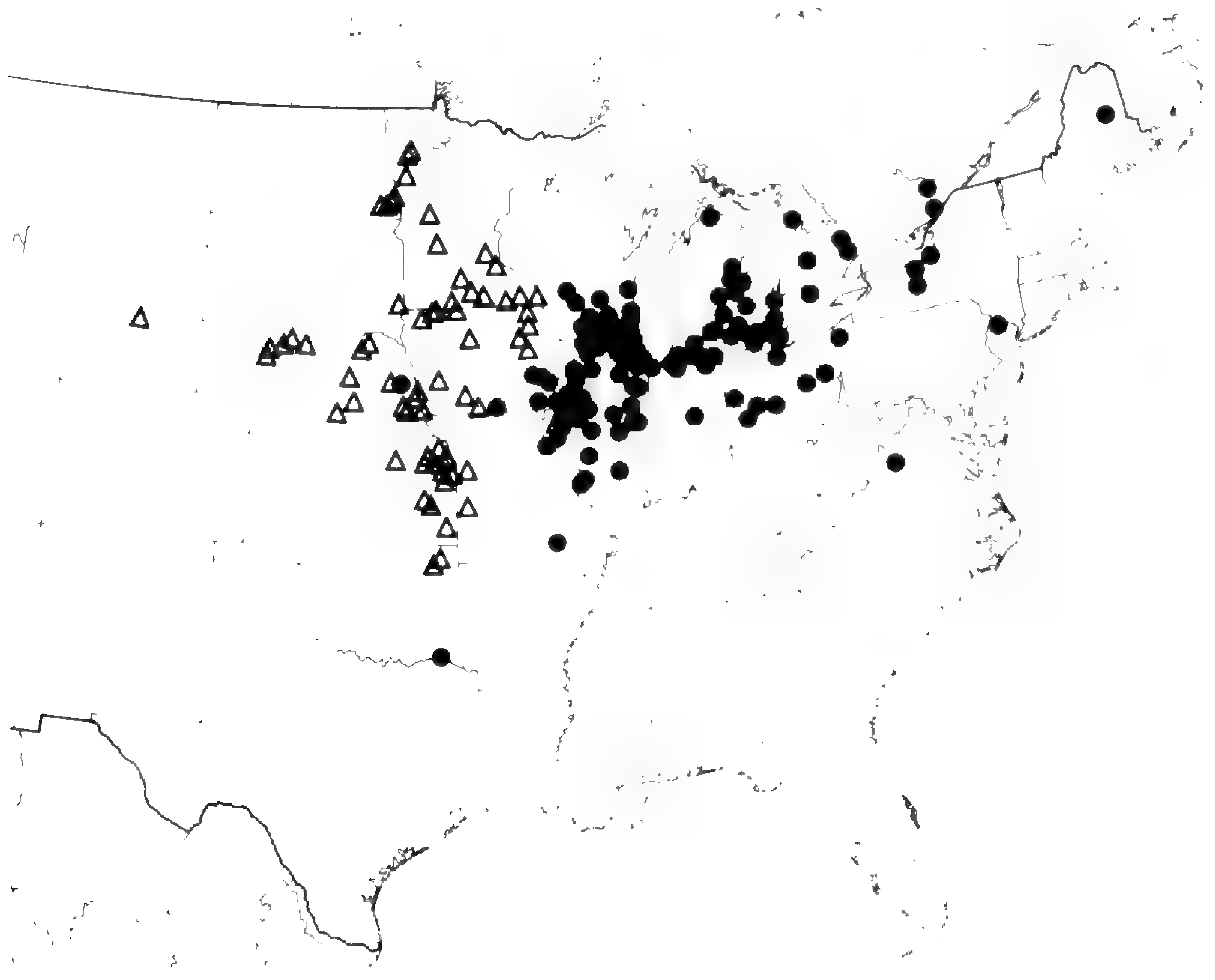

Figure 4. Distributions of *Platanthera praeclara* (triangles) and *P. leucophaea* (dots).

disjunct communities and isolated populations of prairie species. Populations of *Platanthera leucophaea* in the East probably were established during this period of pronounced prairie influence and are consequently relictual. Insofar as the prairie peninsula is a recent extension of the western prairies, the present distribution of *P. leucophaea* may have developed more recently than that of *P. praeclara.* This situation is significant and may provide evidence of the origin of *P. leucophaea.*

The column of *Platanthera leucophaea* appears to represent an advancement over that of *P. praeclara.* Proboscis deposition should lead to greater reproductive success through utilization of a greater diversity of pollinators. This situation may be related to the distribution of *P. leucophaea* in the prairie peninsula. This species may have arisen from *P. praeclara* and colonized northeastward as the prairie peninsula developed. Its ability to utilize a variety of pollinators would have been of great significance as it colonized new types of habitat and encountered different faunas. Regardless of the time of its origin, these adaptively significant features enabled *P. leucophaea* to expand its range across an ecologically diverse and unstable region and to occupy a variety of habitats. In contrast, *P. praeclara* remains restricted to essentially a single habitat in a region that is biologically and climatically uniform and stable.

It is significant that *Platanthera grandiflora* and *P. psycodes* display a similar pattern. The eye-depositing *P. grandiflora* is relatively restricted in range, essentially limited to the Appalachian region, whereas the proboscis-depositing *P. psycodes* is widespread throughout the glaciated Northeast. It appears that this species pair mirrors the pattern in the prairie species. The reproductively more efficient *P. psycodes* has been able to colonize a wide, diverse geographic region, whereas its more specialized relative has been comparatively less successful. Hence, an increase in reproductive efficiency through evolution of less specific pollination mechanisms may be a potential in the group which has been repeatedly exploited as a strategy in response to climatic and biotic fluctuations.

A NOTE ON COMMON NAMES

The great popular appeal of the prairie fringed orchids and the consideration given these plants under federal, state, and provincial endangered species programs will doubtless result in the appearance of new common names now that two species are recognized. Accordingly, we appeal for adoption of the names "Eastern Prairie Fringed Orchid" and "Western Prairie Fringed Orchid" for these two species. These names are simple, descriptive, and based on past usage.

ACKNOWLEDGMENTS

We thank the curators and staffs of the herbaria that lent specimens for this study, including AMES, BKL, BM, DAO, DEK, F, ILL, IND, KANU, KNOX, KSC, MICH, MIN, MO, MWI, NEB, NY, NYS, OCLA, OKL, OKLA, OS, PH, SDU, TEX, UARK, UMO, US, WIS. We also appreciate the efforts made to locate Nuttall, Hale, and Leavenworth specimens and other critical collections at CGE, DUKE, DWC, E, G, K, LIV, LSU, MANCH, NLU, NO, OXF, VDB. A number of persons provided information on plants in their areas, assisted in the field, and contributed specimens and live plants: F. W. Case, Jr., Saginaw, Michigan; P. M. Catling, Agriculture Canada; P. Currier, Platte River Whooping Crane Habitat Maintenance Trust; L. K. Magrath, College of Science and Arts of Oklahoma; T. L. McCabe, New York State Museum; D. Roosa, Iowa State Preserves Advisory Board; W. Smith, Minnesota Natural Heritage Program; R. Warner, North Dakota Natural Heritage Program; T. Wieboldt, Virginia Polytechnic Institute. Location of the Wyoming station of *Platanthera praeclara* was established and brought to our attention by W. F. Jennings, Boulder, Colorado. Live *Manduca* pupae were generously provided by J. Keesy, University of Wisconsin, Madison. We are indebted to E. A. Gossen, New York State Museum Library, for digging out much critical biographical and archival material, and to the New York Botanical Garden Library for providing the Torrey correspondence for study. Drawings in Figure 1 are by Linda Lobik. We wish to thank P. M. Catling for his thoughtful review of the manuscript.

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C. J. S.
BIOLOGICAL SURVEY
NEW YORK STATE MUSEUM
THE STATE EDUCATION DEPARTMENT
ALBANY, NEW YORK 12230

M. L. B.
DEPARTMENT OF PLANT BIOLOGY
UNIVERSITY OF ILLINOIS
URBANA, ILLINOIS 61801

NEW COMBINATIONS IN THE SOLANACEAE

Rafael Castillo and
Richard Evans Schultes

1. In 1977, A. T. Hunziker reestablished the generic name *Merinthopodium* Donnell Smith, distinguishing the genus from *Markea* L. C. Richard by its dorsifixed anthers exceeding the corolla tube and by the corolla which is valvate, not quincuncial in aestivation (Hunziker: Kurtziana 10 (1977) 30–31). He cited four species from Central America and one from Colombia. He furthermore cited *Markea vogelii* Cuatrecasas from Colombia, noting that "...I do not find any difference between this species and *Merinthopodium uniflorum* (Lundell) A. T. Hunziker, except that the anthers are somewhat longer."

An examination of *Merinthopodium uniflorum* indicates that the lower surface of the leaves is covered with sharp-pointed rigid trichomes that are basally swollen and almost a millimeter long. When these hairs are broken, they leave very conspicuous pointed scars. The rigidly coriaceous, subobtuse leaves also have an abundance of glandular papillae, especially beneath.

In our work of identifying the solanaceous plates of the Real Expedición Botánica del Nuevo Reino de Granada, we have discovered an illustration (Plate No. 7367) which we believe represents a species hitherto included in *Markea: M. vogelii* Cuatrecasas. In the United States National Herbarium there is a specimen representing this species concept—the type collection, *Vogel 159* from Monteredonda, Departmento de Cundinamarca, Colombia, 1800 m., October 13, 1956.

This collection has thin, flexible leaves that are attenuately acute. The leaves and twigs are devoid of hairs or glandular scars. Additional collections undoubtedly will provide further differences between these two concepts, but we believe that these two differences are sufficient to indicate that *Merinthopodium uniflorum* of Mexico and *Markea vogelii* of Colombia must be considered distinct species in *Merinthopodium*.

We, therefore, are making the necessary new combination: **Merinthopodium vogelii** (Cuatrecasas) Castillo et R. E. Schultes, *comb. nov.*

Markea vogelii Cuatrecasas, Journ. Wash. Acad. Sci. 49: 269, fig. 1c. 1959: TYPE: *Vogel 159,* US.

We are pleased to express our gratitude to Dr. José Cuatrecasas for his graciously offered help.

2. Research in identifying the plates of the Expedición Botánica has revealed the need for another new combination. Plate Nos. 3733 and 3734 represent a species hitherto known as *Saracha vestita* Miers.

In 1973, J. L. Gentry reestablished the generic name *Jaltomata* Schlechtendahl (Phytologia 27: 286. 1973). He made new combinations for two Central American species but none for any from South America.

Jaltomata vestita (Miers) Castillo et R. E. Schultes, *comb. nov.*

Saracha vestita Miers, Ann. and Mag. Nat. Hist., ser. 2, 3: 449. 1849.

During our research into the Solanaceae, we have discovered that another species which has been included in *Saracha* should now be transferred to *Jaltomata.* Consequently, the following new combination is proposed:

Jaltomata glandulosa (Miers) Castillo et R. E. Schultes, *comb. nov.*

Saracha glandulosa Miers in Ann. and Mag. Nat. Hist., ser. 2, 3: 450. 1849.

R. C.
UNIVERSIDAD PEDAGÓGICA
Y TECHNOLÓGICA DE COLOMBIA
TUNJA, COLOMBIA

R. E. S.
BOTANICAL MUSEUM OF HARVARD UNIVERSITY
CAMBRIDGE, MA 02138

BOOK REVIEW

DAVID B. LELLINGER with photographs by A. Murray Evans. 1985. *A Field Manual of the Ferns and Fern-Allies of the United States and Canada.* ix + 389 pp. Smithsonian Institution Press, Washington, D. C. ($45.00 cloth; $29.95 paper)

This book is a valuable addition to the manuals on ferns for both professional and amateur botanists. The introductory material is presented in a way that can be understood by those not familar with the biology of ferns. The glossary at the back of the book is very clear and has illustrations of characters difficult to describe. Once to the keys there are a number of characters used to facilitate choices, rather than dependence on one character. The keys are bracketed keys and each dichotomy indicates the previous choice made; thus steps can be retraced. The descriptions are precise; thus the book should be useful to botanists at all levels of expertise. The innovation of the hybrid charts at the end of the book should prove to be a useful addition to fern manuals.

There are two pairs of photographs which have been misplaced: 386 and 388 (*Nephrolepis exaltata* and *N. biserrata*) are reversed as are 399 and 400, (*Marsilea macropoda* and *M. vestita*). The photographs are excellent overall. One wishes that the penny used for scale in 75 and 96 could have come out of the photographer's pocket more often since for someone unfamilar with the plants it would be helpful to know how large or small they really are. Many of the photographs are not very useful for diagnostic characters between species, especially in the *Lycopodium* species: e.g. *alopecuroides* and *prostratum*, and the *tristachyum* complex. A beginner will be hard pressed to distinguish these species. Perhaps some diagnostic sketches or a statement in the descriptions as to species easily confused and the particular characters to check would be useful in future editions. For the serious pteridologist there are some as yet undescribed species in the book under *Botrychium* and *Polypodium* but that does not decrease its usefulness for identification.

The checklist might be confusing at first since the generic names are indented but the specific epithets are not. This makes some of the genera difficult to find quickly and I would prefer the genera to be in boldface or capitals.

Overall I find the book extremely useful. It lists all the fern species in the area covered and includes much pertinent information. An extensive bibliography leads one on to more detailed studies. The photographs are very attractive and each one is worth much more space than it has been given. Indices of both common and scientific names are provided. Much work and care has gone into the production of this manual and it will be referred to again and again by botanists interested in the lower vascular plants of North America.

JUDITH E. SKOG
BIOLOGY DEPARTMENT
GEORGE MASON UNIVERSITY
FAIRFAX, VA 22030

JOINT FIELD MEETING: June 15–18, 1986

The Annual Joint Field Meeting of
The Northeastern Section of the Botanical Society of America
The Philadelphia Botanical Club, and
The Torrey Botanical Club
will be held June 15 to 18, 1986 at Paul Smith's College. Paul Smith's College is located in the upper Adirondacks, on the shore of Lower St. Regis Lake. Accommodations are in dorms built for the 1982 Olympics, with private baths. Additional standard dorm accommodations are available.

Trips to sites of interest will be led by authorities on the Adirondack flora. Evening lectures will provide local background and history. Many historical and recreational facilities are located in the vicinity.

Prior registration is advised. Information is available from:

Dr. Charles Burch
Wells College
Aurora, NY 13026

Vol. 88, No. 853, including pages 1–156, was issued January 30, 1986

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Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

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Cover Illustration

An original drawing, seemingly the only one surviving and perhaps the only one ever done for publication by Merritt Lyndon Fernald, used in part to illustrate his article on cranberry species which appeared in RHODORA No. 48 (Fernald, M. L. 1902. The variations and distribution of American cranberries. Rhodora 4: 231–237 & Plate 40). The drawing was rescued from a wastebasket by Dr. Bernice Schubert; it now hangs in the office of Dr. Carroll E. Wood at A. The original Plate 40 caption reads as follows: Fig. 1, *Vaccinium Vitis-Idaea;* fig. 2, *V. Vitis-Idaea,* var. *minor;* fig. 3, *V. Oxycoccus;* fig. 4, *V. Oxycoccus* var. *intermedium;* fig. 5, *V. macrocarpon.*

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THE MORPHOLOGY AND CYTOLOGY OF *POLYSTICHUM* × *POTTERI HYBR. NOV.* (= *P. ACROSTICHOIDES* × *P. BRAUNII*)

DAVID S. BARRINGTON

ABSTRACT

The hybrid between *Polystichum acrostichoides* and *P. braunii* is common but overlooked in Vermont. Based on a qualitative analysis, the hybrid is structurally intermediate for most traits, but character states are not predominantly medial or nearer to those of tetraploid *P. braunii*. Indusia of the hybrid are much larger than those of either progenitor, suggesting a summation of development programs for indusial development. Stomates of the triploid hybrids are intermediate and nearer to those of *P. braunii* in size, but those of diploid *P. acrostichoides* are unexpectedly larger than those of tetraploid *P. braunii*. Chromosome counts confirm that the hybrid is commonly triploid, and that non-homologous pairing is high, as reported for other *Polystichum* hybrids (mean number of bivalents is 21.7). The hybrid is described and named as *P.* × *potteri*.

Key Words: *Polystichum*, hybrid, fern morphology, Vermont

INTRODUCTION

During the past few years botanists have frequently encountered the hybrid between *Polystichum acrostichoides* and *P. braunii* at Vermont stations where both parents are common. Review of herbarium materials has yielded a set of these hybrids from the northern Appalachians, all determined as *P. braunii*. This hybrid now appears to be common, at least in the Green Mountains, but overlooked because it shares several features, notably a similar lamina dissection, with its tetraploid progenitor, Braun's Holly Fern (*P. braunii*). In this paper, I provide basic structural, cytological, ecological, and geographical documentation for the hybrid. Since I argue that commonly occurring entities in nature need names, I am also providing an epithet, type designation, and Latin description.

The first and only previous report of the native hybrid between *Polystichum acrostichoides* and *P. braunii* was by Thompson & Coffin (1940). It was based on a single small sporophyte that they encountered in Smuggler's Notch, Vermont during the summer of 1937. Thompson and Coffin used 18 characters to evaluate the hybrid. They reported that the hybrid shared seven character states with *P. acrostichoides* and three with *P. braunii.* Of the seven character states reported as intermediate, three were nearer to *P. acrostichoides,* three were medial, and one was nearer to *P. braunii.* One character state was not intermediate (leaf length was shorter than that of either progenitor). This relatively early report provided no information on cytology or variation in spores or sporangia.

Morzenti (1962), in developing her ideas on pseudomeiotic sporogenesis, described the cytology of a *Polystichum acrostichoides* × *P. braunii* hybrid from the garden of Harold Rugg (at Hanover, New Hampshire), thought to be a derivative of the plant discovered by Thompson and Coffin. At meiosis the Rugg plant had 41 bivalents and 82 univalents (two of four sets of chromosomes pairing). Assuming that the *P. acrostichoides* parent was diploid ($x = 41$) and the *P. braunii* parent was tetraploid ($x = 82$) (Löve et al., 1977), the origin of the Rugg plant must have been via an anomalous cytological pathway. Morzenti suggested that the Rugg plant was tetraploid (rather than triploid as expected) because *P. acrostichoides* had contributed an extra set of chromosomes, either from a tetraploid sporophyte or, according to Morzenti (1962), from "duplication of the normal diploid genome of that species in the hybrid" (for instance, via an unreduced gamete). The tetraploid plant from Rugg's garden had some sporangia that yielded 16 giant, viable spores. These giant spores yielded gametophytes with spermatozoa and archegonia, but no sporophytes.

SYSTEMATIC TREATMENT

Polystichum × potteri Barrington, *hybr. nov.* = *Polystichum acrostichoides* (L.) Roth × *P. braunii* (Spenner) Fée.

DIAGNOSIS: Hybrida sterilis e Polysticho acrostichoide atque P. braunii prodiens, ab illo differt foliis pinnatisectis vix supra medium latissimis apicem versus non contractis, carenti foliis laxis sine sporangiis; ab hoc petiolis et pinnis basalibus longioribus. Indusia hybridae indusiis parentium grandiora.

HOLOTYPE: Vermont, Orange Co., Strafford, Beacon Hill; low ledges in shady maple woods above Chadsey residence, *Barrington 939:* VT.

PARATYPES: The Appendix provides citations of the numerous paratypes.

Stem prostrate, short-creeping, branching at irregular intervals, bearing a single whorl of rigidly ascendent leaves. Leaves long-petiolate, chartaceous to coriaceous; lamina long-lanceolate, narrowed to a truncate base, apically attenuate, but not abruptly narrowed into the fertile apical portion (Figure 1); lamina dissection twice-pinnate, but the distal half of most pinnae merely pinnatifid to pinnatisect (Figure 2); basal acroscopic pinnules of most pinnae crenate to pinnatifid, one-third to twice again as long as the nearest more distal pinnules; pinnules crenate and long-spinulose, ascendent along the pinna-rachis (costa axis attached at 50–60 degrees from the pinna-rachis). The distal half or two-thirds of each lamina with approximate sori, (lax trophophylls not seen). Indusia irregularly crenate-margined, ca. 1.0 mm in diameter. Sporangia commonly but not always indehiscent; tapetal remnants clinging to sporangium interior. Spores irregular, pale.

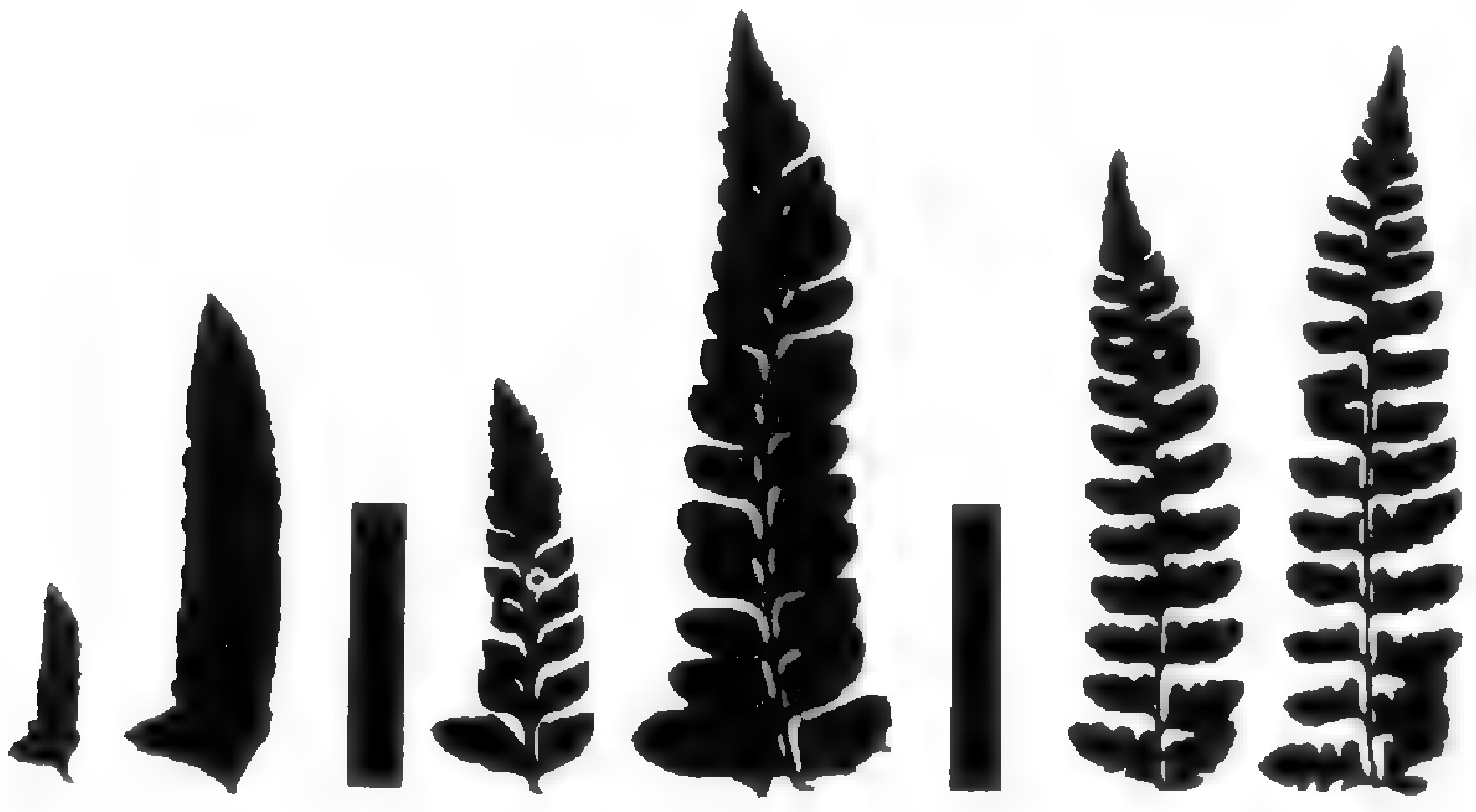
Indument of petioles and rhizome apex a dense cover of broad-lanceolate, amber to stramineous scales with a few short marginal setae and scurf like that of the rachis. Rachis scurf abaxially lanceolate to long-lanceolate, amber to stramineous, weakly to heavily short-setate, more or less descendent along the rachis; adaxially filiform and stramineous. Leaf-surface indument abaxially well developed, of long (ca. 0.7 mm) very narrow-lanceolate scurf.

ETYMOLOGY: *Polystichum* × *potteri* is named for the late Henry Potter of West Rutland, Vermont, lifelong student of the Vermont fern flora and one of the state's finest naturalists, who was still active last field season at 94.

I have found it useful to develop a set of categories for the qualitative character states encountered in the hybrids. Relative to those of its progenitors, hybrid character states are necessarily of three sorts:

1

2



Figures 1 and 2: Figure **1.** Leaf silhouettes of *Polystichum* species: from left to right, *P. acrostichoides* (*Barrington #1123,* original leaf length 63 cm). *P.* × *potteri (Barrington #939,* original leaf length 77 cm), and *P. braunii* (*Barrington #1138,* original leaf length 66 cm).

Figure **2.** Pinna silhouettes of *Polystichum* species (left pinna of each pair from three-quarters up lamina, right pinna from center): from left to right, *P. acrostichoides* (*Barrington #1123*), *P.* × *potteri* (*Barrington #939*), and *P. braunii* (*Barrington #1138*). Bars = 2cm.

shared with one of the progenitors, intermediate, or anomalous (that is, neither shared nor intermediate). Intermediate character states are more or less variable between the two progenitors. The less variable intermediate states are either medial (clustered at the mean between the progenitors) or nearer one or the other of the two progenitors.

Twenty-two qualitative characters were scored for the two species and their hybrid (Table 1). Comparison of the hybrid with its progenitors revealed that the hybrid shared five character states with *Polystichum braunii,* but only two with *P. acrostichoides.* Thirteen character states were intermediate between the two progenitors: three of these were nearer *P. acrostichoides,* eight were medial, two were nearer *P. braunii,* and one was variable. A single character state, indusium diameter, was anomalous—it was larger than that of either progenitor. In sum, the characters assessed were variable in their expression relative to the two progenitors.

An Anderson hybrid index (Anderson 1936, 1949) was computed for *Polystichum* × *potteri,* using the qualitative character states (Table 1). Contrary to Anderson's usual approach, the index was computed for the composite characters diagnostic of the group of hybrids as a whole and not for the individual character states of each hybrid. Based on the hybrid index, the hybrid is intermediate and slightly closer to *P. braunii* than to *P. acrostichoides* (57th percentile, given *P. braunii* is the 100th percentile).

An Anderson hybrid-index score was computed for the sporophyte from Rugg's garden that was presumably the source of Morzenti's tetraploid count. (Only characters available from the herbarium sheets were possible to score.) The MICH collection was at the 42nd percentile, and the GH collection was at the 41st percentile; that is, both were slightly closer to *P. acrostichoides* than were the triploid plants of the hybrid. The Thompson & Coffin specimen at GH was scored at the 61st percentile, that is similar to the composite index for the hybrids.

Guard-cell measurements, which were done to corroborate ploidy-level information derived from cytology, yielded unexpected results. Guard-cell pair length and width of the diploid species were a bit larger than those of the tetraploid species, rather than a bit smaller (Table 2). Guard-cell measurements of the triploid hybrids

Table 1. Structural features of *Polystichum* × *potteri* and its progenitors compared (Anderson Hybrid Index scores in parentheses: 0 = shared with *acrostichoides*; 1 = intermediate and nearer *acrostichoides*; 2 = medial; 3 = intermediate and nearer *braunii*; 4 = shared with *braunii*.)

Character	*acrostichoides* (a) (all 0)	hybrid	*braunii* (b) (all 4)
Petiole length	long	intermediate, nearer a (1)	short
Lax trophophylls	present	shared with b (4)	absent
Attitude of fertile leaves	stiffly ascendent	shared with a (0)	laxly ascendent
Lamina texture	coriaceous	medial (2)	herbaceous to chartaceous
Evergreenness	evergreen	intermediate, nearer a (1)	deciduous to unevenly evergreen
Lamina base width	nearly = medial width	medial (2)	one third the medial width
Point of maximum lamina width	near lamina base	medial (2)	above the middle of the lamina
Lamina dissection medial	1-pinnate to 1-pinnate, pinnatifid	intermediate, nearer b (3)	1-pinnate, pinnatisect
Angle of costae	45°	medial (2)	80°
Stomate length	long	intermediate, nearer b (3)	short
Rachis-scale setae	present	intermediate, nearer a (1)	rare
Rachis-scale texture	dull	intermediate, various (2)	lustrous
Adaxial rachis scales	narrow-lanceolate to lanceolate	shared with b (4)	filiform

Table 1. Continued

Character	*acrostichoides* (a) (all 0)	hybrid	*braunii* (b) (all 4)
Abaxial lamina scurf size	small	medial (2)	large
Abaxial lamina scurf shape	filiform	intermediate, nearer a (1)	narrow-lanceolate
Lamina scurf frequency	rare	medial (2)	abundant
Fertile lamina portion	contracted	shared with b (4)	not contracted
Receptacle shape	round to elongate	shared with b (4)	round
Sorus proximity	confluent	medial (2)	remote
Receptacle sclerenchyma	abundant	shared with b (4)	weak
True indusium diameter	small	not intermediate (not indexed)	small
True indusium shape	entire	medial (2)	crenate
Anderson Hybrid Index Totals	0	48	84

Table 2. Guard-cell pair measurements in μm for *Polystichum* × *potteri* and its progenitors (n = 30 guard cell pairs measured for each sporophyte)

PARENTS AND PUTATIVE TRIPLOIDS

Locality	*acrostichoides*	hybrid (putative triploids)	*braunii*
Wheelock			
DSB #	1172	946	1175
mean length (s. d.)	54.1 (3.48)	51.3 (3.45)	49.0 (2.67)
mean width (s. d.)	40.6 (1.93)	34.0 (2.36)	31.8 (2.81)
Strafford			
DSB #	1185	939 (holotype)	1183
mean length (s. d.)	52.6 (3.20)	51.1 (3.20)	47.7 (3.79)
mean width (s. d.)	37.9 (2.57)	32.3 (2.13)	31.2 (1.98)
Barnard			
DSB #	1144	1097	1119
mean length (s. d.)	54.4 (4.09)	48.0 (2.82)	46.7 (3.10)
mean width (s. d.)	37.1 (2.54)	31.0 (2.16)	31.0 (1.85)
Mean for all sites			
mean length (s. d.)	53.6 (0.97)	50.0 (1.83)	47.8 (1.14)
mean width (s. d.)	38.6 (1.88)	32.5 (1.52)	31.2 (0.38)

PUTATIVE TETRAPLOID

Rugg s. n. (GH)		Rugg s. n. (MICH)	
mean length (s. d.)	59.8 (5.36)	mean length (s. d.)	64.0 (4.43)
mean width (s. d.)	12.5 (0.78)	mean width (s. d.)	42.0 (2.26)

were nevertheless intermediate and nearer to those of *Polystichum braunii.* Guard-cell dimensions of the Rugg collections at GH and MICH (both presumed to be vouchers for Morzenti's tetraploid hybrid) were larger than those of any other plants in the sample (Table 2).

One unusual structural variant was seen among the hybrids collected in Vermont. The basal pinnae in most leaves of *Barrington 1155* (VT) are the same length as the widest pinnae in the blade, but the next few pinnae acropetally are irregular in length: some are short like those at the base of *Polystichum braunii* leaves; others are long like those of *P. acrostichoides.*

GEOGRAPHY & ECOLOGY

Polystichum × *potteri* is known from Quebec, Nova Scotia, New Brunswick, New Hampshire, Vermont, New York, and Pennsylvania. In Vermont the hybrid is found in cool, wet forests from 1000 to 3000 feet. The hybrids are often found in ice-carved notches and on wet, steep, rocky slopes—both habitats characterized by unstable, thin-soiled substrates. Both parents are present at all of the Vermont stations known to the author.

Polystichum braunii has a circumboreal distribution (Hultén, 1962). Compared with other circumboreal ferns, it is relatively northern in distribution. For instance, in Europe it is confined to the maritime parts of Scandinavia and montane regions, and in western North America it is entirely coastal and northern. In Vermont *P. braunii* is limited to wet, disturbed substrates in forests at altitudes above 1000 feet. In contrast, *P. acrostichoides* is endemic to North America. It is a common species of woodlands in eastern North America where it is best developed on wooded, thin-soiled slopes, which are frequently disturbed. The hybrid between the two was encountered in Vermont at fairly high altitudes where *P. braunii* (near its lower limits) and *P. acrostichoides* (near its upper limits) occupy the same habitat.

Eight of the 14 Vermont sites yielded only a single hybrid sporophyte despite careful searching, whereas two sites had two sporophytes each, one had five, one had ten, and one had twenty-four. Some of the sporophytes at these sites are clustered and appear to be part of a single clone, suggesting that vegetative reproduction increases numbers of plants in populations. However, the large populations are for the most part well spread out over the terrain, from which I infer that they are separate genets, not ramets derived from branching of stems.

CYTOLOGY & SPORE VARIATION

Seventeen sporophytes yielded cytological preparations with univalents. The three sporophytes yielding counts were triploids with univalents and various numbers of bivalents ranging from 19 to 26 (Table 3; Figure 3–6). During early anaphase the bivalents are slow to separate, resulting in the characteristic early anaphase figures

Table 3. Chromosome number and pairing behavior in *Polystichum* × *potteri*

Barrington Collection Number & Sporocyte Letter	Univalents	Bivalents	Trivalents
939A	71	26	0
939B	81	21	0
942A	74	23	1
942B	77	23	0
942C	87	18	0
942D	79	22	0
1094A	85	19	0
Mean	79.1	21.7	0.14
(s. d.)	(5.73)	(2.69)	(0.37)

also illustrated in European work on *Polystichum* hybrids (Manton and Reichstein, 1961; Sleep and Reichstein, 1967). Chromosome segregation is irregular in meiosis, so that micronuclei are common in the resultant spores.

The spores resulting from meiosis are for the most part wrinkled and irregular in shape. Giant spores resulting from inclusion of all the meiotic nuclei in a single cell, like those observed by Morzenti (1962), were common in some of these triploid hybrids (*Barrington 909* VT). Indehiscent, pale, collapsed sporangia are useful in field identification of the hybrids, but indusia only rarely fail to evert as in *Dryopteris* hybrids (Wagner and Chen, 1965). Some of the sporangia of the hybrids open as the summer progresses; the proportion of sporangia which open varies with the sporophyte. Pale bits of tapetal material which cling to the interior of the opened sporangia of the hybrid, but which are absent from those of the parents, are diagnostic. These tapetal remnants were seen in all herbarium specimens of hybrids at VT.

DISCUSSION

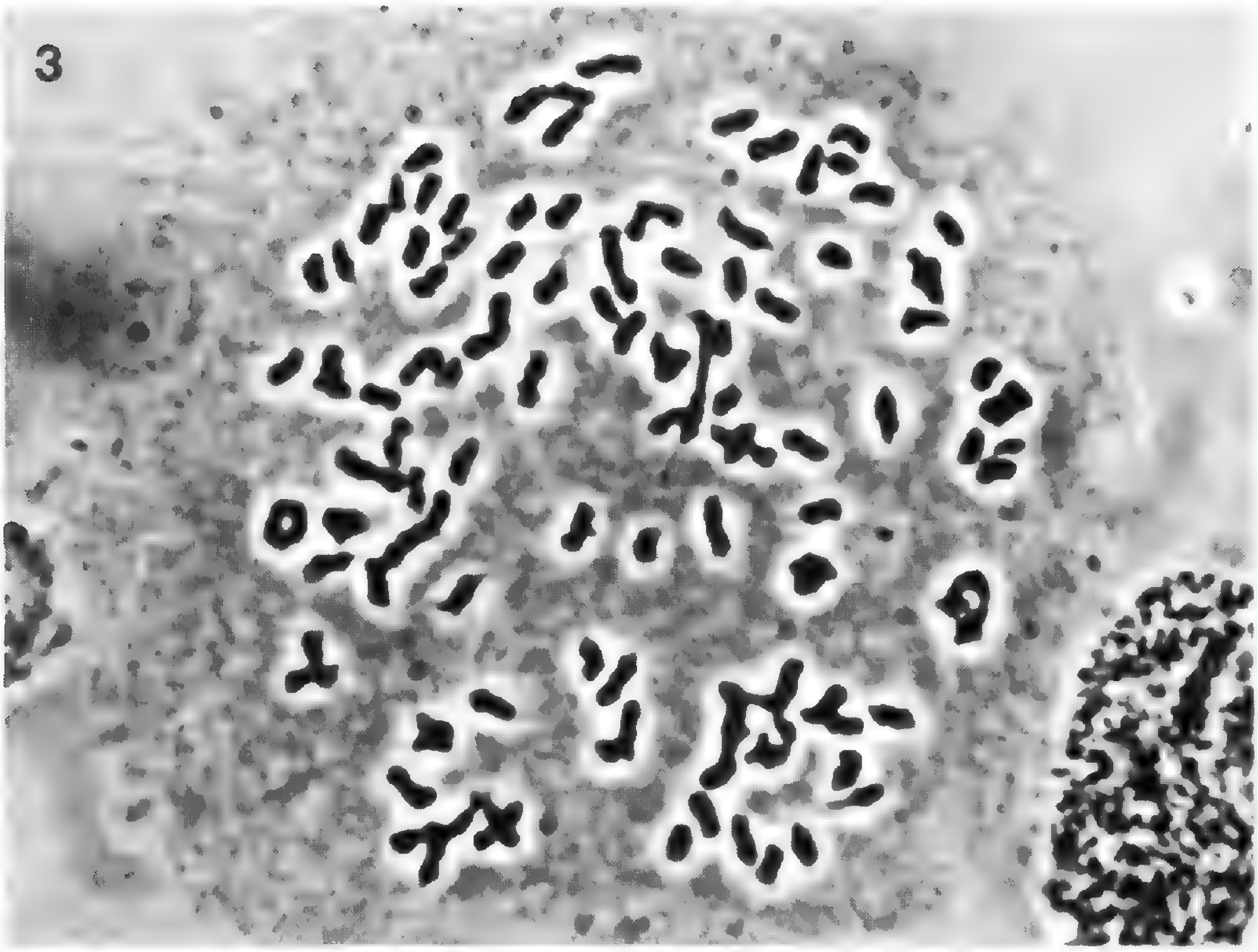
Polystichum × *potteri* has been largely overlooked because it superficially looks so much like its tetraploid progenitor, *P. braunii*. Lamina dissection is probably the single most important character used in determining northeastern North American specimens of *Polystichum* and, in this character, the hybrid is intermediate and nearer *P. braunii*.

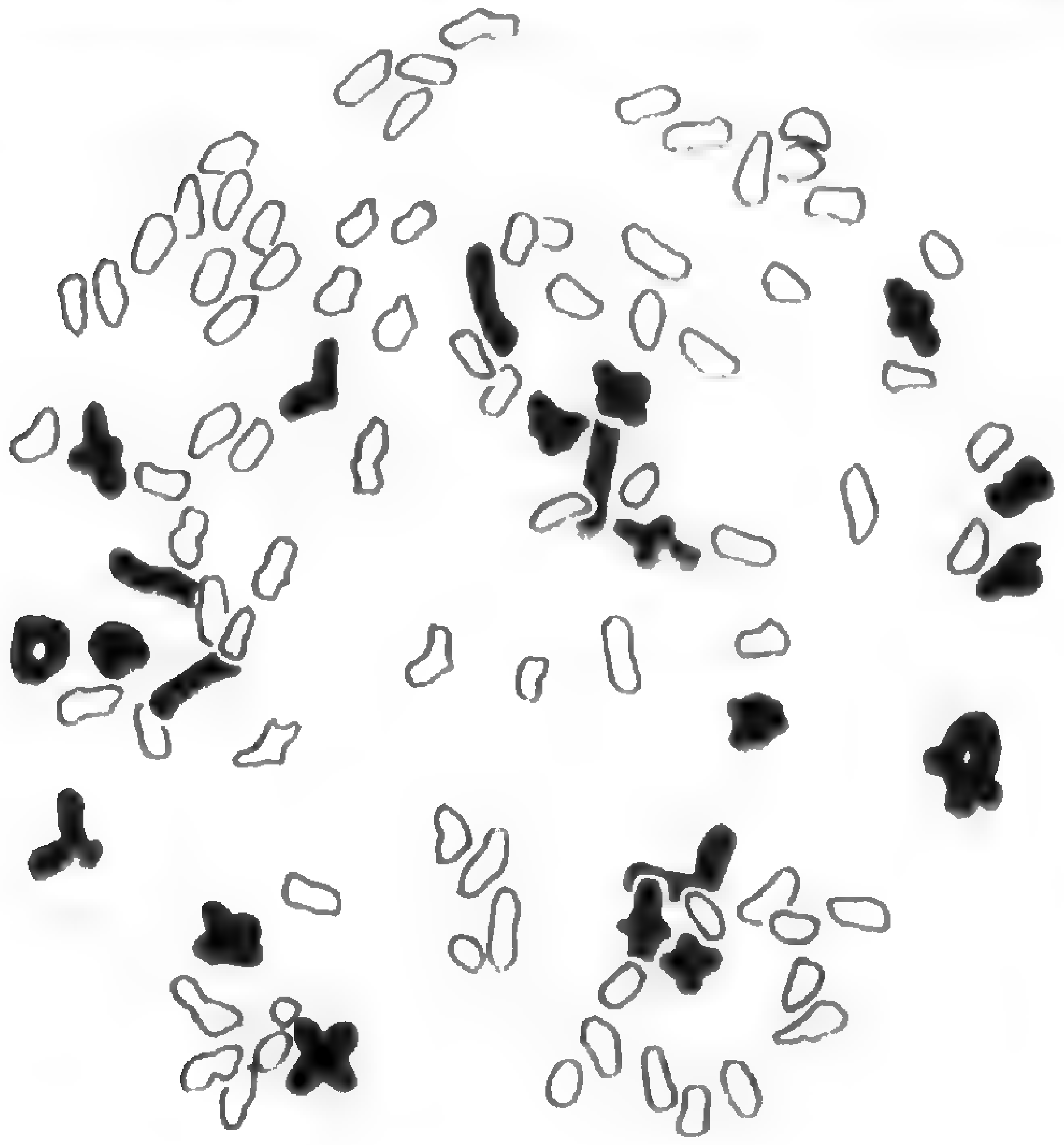
Intermediacy of sterile hybrids, assumed to be F_1s only, often serves as the basis for hypothesizing hybrid ancestry of plant lineages (Wagner, 1983), but scoring of hybrids is often based on intuition rather than on character analysis. Hybrids between tetraploids and diploids are commonly expected to approach the tetraploid in structure because the tetraploid is genetically represented twice, but the diploid only once. However, all of the various possible character states are represented among the characters surveyed in the present hybrid. Although medial states are most common, they only account for about one-third of the characters, and only two characters are intermediate and nearer *Polystichum braunii.* Since structural features are elaborated by various genetic systems, most of them polygenic, a complex array of character states is to be expected in hybrids. A quantitative analysis of the character states of progenitors and hybrids would serve as the basis for a better understanding of hybrid character states in *P.* × *potteri.*

The Anderson hybrid-index scores for the Rugg specimens (GH, MICH) were closer to *Polystichum acrostichoides* than was the composite hybrid-index score. Though these data are qualitative, (and the tie of the tetraploid count to these Rugg specimens is circumstantial) they suggest that an extra set of chromosomes from *P. acrostichoides* resulted in leaf characteristics more like those of the diploid species. The hybrid-index score for the Thompson & Coffin specimen suggests that it was a triploid, and consequently probably not from the same plant as the Rugg collections (contrary to Morzenti, 1962).

The original qualitative scoring of the hybrid (Thompson and Coffin, 1940) differs from the present one in showing more characters shared with the progenitors and fewer medial character states. Their emphasis was on contrasting the contribution of the progenitors and not on the expression of each of the characters they used.

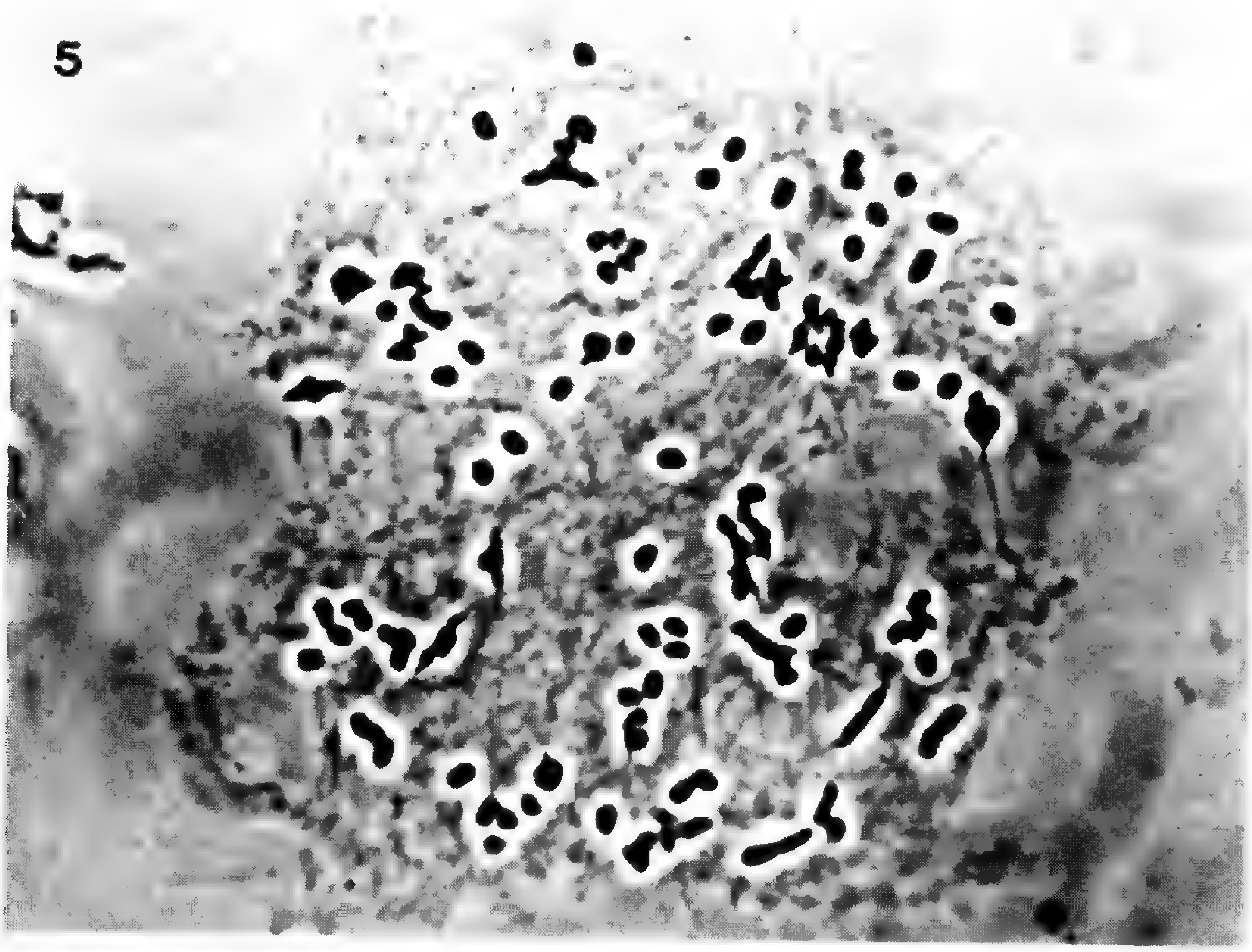
The unusually large indusium size of the hybrid is particularly interesting because it is a novel character state not found in the progenitors. In this case the larger size of the hybrid indusia suggests that the parental genomes have been summed to program for a longer developmental period, generating a larger indusial flange (that is, the round top, not the stalk). The precise developmental sequences in both parents could be compared to investigate this idea. Indusium size is important in characterizing species of *Polystichum* in Mexico (Smith, 1981), so that transformations in this par-





Figures 3 and 4: Figure 3. Late prophase of meiosis I (79I and 22II), *Barrington #942*, 1050X. Figure 4. Camera lucida drawing of sporocyte in figure 3.

5



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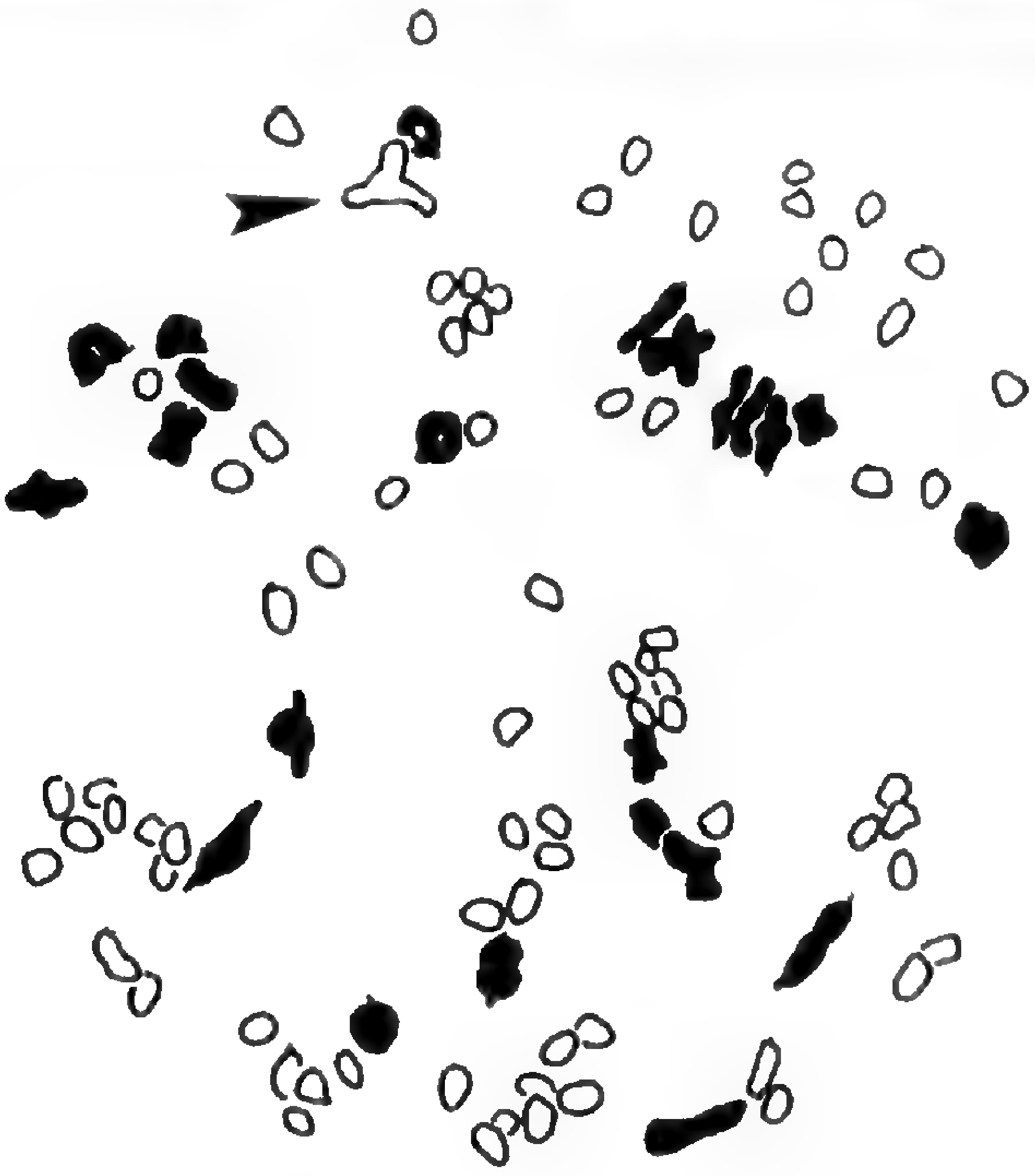

Figures 5 and 6: Figure 5. Metaphase of meiosis I (74I, 23II, 1III indicated with arrow), *Barrington #942,* 800X. Figure 6. Camera lucida drawing of sporocyte in figure 5.

ticular character are possibly important in considering the evolution of the genus as a whole.

The irregular pinnae of *Barrington 1155* can be interpreted as a result of mixed developmental programs from the two parents: broad basal pinnae determined by the *Polystichum acrostichoides* program, followed by pinnae of various lengths resulting from compromises betwen the two parental programs. In contrast, normal hybrids evidence an orderly progression of compromises between the two parental programs, resulting in leaves with regular pinna development intermediate between that of the two parents. Random prevalence of one parental developmental program over another has been invoked to explain a class of irregular features found in hybrids (Barrington, 1985).

The most intriguing character is the stomate size of the three entities. The reasonably good inverse correlation of stomate length with ploidy level known for the species and the triploid hybrid is counter to that demonstrated in classical studies (e.g., Wagner, 1954). Perhaps the diploid progenitor or progenitors of *Polystichum braunii* are both characterized by stomates that are much smaller than those of the native eastern North American *P. acrostichoides.* The large stomate size of the Rugg collections, presumably vouchers for the tetraploid, suggest that the presence of an extra *acrostichoides* genome has an unusual effect on the determination of stomate size.

The contrast between the present triploid chromosome counts and the tetraploid count first reported for this hybrid is remarkable. The hybrid apparently arises most often as a result of fusion of normal gametes of the two parents. A fertile hexaploid race of *Polystichum* × *potteri* may possibly be found, as was a fertile tetraploid population for *Asplenium ebenoides* (Wagner, 1954). Such a plant, backcrossing to *P. acrostichoides,* could have generated the tetraploid documented by Morzenti. No fertile hexaploid hybrids have yet been encountered; all of the large sample of sporophytes recently collected in Vermont are presumed to be sterile triploids, since they all show pale tapetal remnants inside the sporangia. Thus, Morzenti's original hypothesis for the origin of the tetraploid is the simplest, given our present understanding of the hybrid.

Many *Polystichum* hybrids form more bivalents than would be expected as a result of pairing of homologous chromosomes (by definition the result of homoeologous pairing), ranging from an average of 11 (range 6–24) in European *P. braunii* × *lonchitis* (Lovis, 1977) to 26 (range 19–33) in Californian *P. dudleyi* × *munitum* (Wagner, 1973). In *Cystopteris,* Vida (1974) has reported a similar high number of bivalents in the apomictically generated diploid cytological race of *C. fragilis.* Lovis inferred from these data that *Polystichum* and *Cystopteris* polyploids are segmental allopolyploids, that is they share "valuable complex linkages" common to both ancestors, but are otherwise chromosomally divergent. The present hybrid adds to the list of hybrids with unusual levels of pairing. This high level of pairing is of potential interest, since the other polystichums hybridizing with *P. braunii* are much less divergent morphologically. Lovis (1977) reported that Sleep saw similar high levels (overall range nine to 25) of bivalents in synthesized hybrids of *P. acrostichoides* with *P. lonchitis, P. munitum,* and *P. setiferum.*

The origin of *Polystichum braunii* remains an interesting and unsolved problem. None of the five hybrids involving *P. braunii* in Europe and North America shows a full set of bivalents, so that no diploid from these regions is implicated as a progenitor. Though no conclusive information is available from eastern Asia, the close structural similarity to *P. makinoi,* a diploid, suggests that the ancestry of *P. braunii* is Asian.

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DEPARTMENT OF BOTANY
UNIVERSITY OF VERMONT
BURLINGTON, VT 05405-0086

APPENDIX

Exsiccatae for *Polystichum* × *potteri* Barr.

(Specimens determined by D. H. Wagner, Univ. of Oregon, which I have not seen are indicated as det. DW. All others—those at GH, NHN, VT, and YU—are paratypes except for the holotype, *Barrington 939*.)

CANADA: (all det. DW) **Nova Scotia.** Inverness Co.: near Harvard Lakes, *A. Prince & C. Atwood 1442* (DAO). Co. indet.: Folleigh, *M. Malte s. n.* (CAN 216749). **New Brunswick.** York Co.: Keswick, *J. Brittam 26,* (GH). **Quebec.** Brome Co.: Waterloo, *Br. Marie-Anselm s. n.* (DAO). Montmorency Co.: Montmorency Falls, *Macoun 69235 p. p.* (CAN).

UNITED STATES: **New Hampshire.** Coos Co.: White Mountains, quite high, *E. Tuckerman s. n.* in 1843 (GH). **Vermont.** Caledonia Co.: Sutton, W slope of Mt. Hor, *Barrington 777, Zika 3386, 3390* (VT); Wheelock, E face of Mt. Ide, near summit, *Barrington 944, 945, 946, 947, 948, 949, 950, 1084, 1085, 1167* (VT). Chittenden Co.: Underhill, Nebraska Notch, *Barrington 904, 912, 928* (VT); Underhill, base of the chin of Mansfield, *Pursh s. n.* in 1838 (GH). Essex Co.: Brighton, W side of Rt. 114 near Morgan town line, *Barrington 834, Zika 4130* (VT). Lamoille Co.: Eden, Access Road to Belvidere Serpentine Mine, *Hickey 906* (personal herbarium R. James Hickey); E side of Rt. 100 near Lowell town line, *Barrington 909, 959* (VT); Stowe, *F. Bumstead s. n.* (YU); Cambridge, Smuggler's Notch, *Barrington 918* (VT), garden specimen from Smuggler's Notch, *R. H. Thompson & R. L. Coffin s. n.* in 1940 (GH), *J. Churchill s. n.* (MO 1055822, det. DW). Orange Co.: Braintree, *J. Bates 496* (YU); Brookfield, E side of Brookfield Gulf, 1200 feet, *Barrington 1081, 1082, Zika 7196, 7199* (VT); Strafford, Beacon Hill, *Barrington 939* (holotype), *940, 941, 942, 943* (VT). Orleans Co.: Westmore, E side of Mt. Hor, 1500 feet, *Zika 7348* (VT); Town indet., Willoughby Mt., *J. Churchill s. n.* (MO 1055821, det. DW). Rutland Co.: Sherburne, Shaw Hill Brook ravine, 1550 feet, *Barrington 750* (VT); W slope of Wolf Hill, *Barrington 749a* (VT). Windsor Co.: Barnard, Barnard Gulf, *Barrington 1091, 1092, 1093, 1094, 1096, 1097, 1098, 1099, 1100, 1103, 1105, 1106, 1116, 1125, 1131, 1134, 1135, 1140, 1143, 1148, 1151, 1153, 1155, 1157* (VT); same locality, *E. Kittredge s. n.* (MO 993604, det. DW); Cavendish, W side of Proctorsville Gulf, *Barrington 898* (VT); Sharon, Honey Brook Ravine, *Barrington 990* (VT); Woodstock, *Miss Strong s. n.* (HNH). **New York.** (all det. DW) Delaware Co.: Arkville, *P. Wilson s. n.* (NY). Co. indet.: Ox Clove, Catskill Mts., *C. Lown s. n.* (NY). **Pennsylvania.** Sullivan Co.: Ganoga Glen, *H. Pretz 3922, 3923a,* (MICH, det. DW). Wayne Co.: Scott Twp., NE side of Schrawder Mt., 1 mi N of Island Lake, *W. Dix s. n.* (US, det. DW); NE slope of Shrawder Mt., *E. Wherry s. n.* (GH; US, det. DW). Starrucca, Lake Shehawken, *W. Dix s. n.* (GH); Sterling, *R. C. Harlow s. n.* in July, 1939 (GH), in July 1941 (GH), Gas Hollow, 2 mi. from Jericho (GH).

PLANTAGO MARITIMA AND *CAREX MACKENZIEI* NEW FOR SASKATCHEWAN: ADDITIONAL RARE INLAND STATIONS FOR TWO SEACOAST SALT MARSH SPECIES

Vernon L. Harms, Donald F. Hooper, and Les Baker

ABSTRACT

Plantago maritima L. and *Carex mackenziei* Krecz., two seacoast salt marsh species rare at inland stations, are reported from the lower Carrot River valley of east-central Saskatchewan, Canada as new to the flora of the province. Taxonomic considerations for *Plantago maritima* and phytogeographical observations and comments for both species are included.

Key Words: *Plantago maritima, Carex mackenziei,* inland stations, salt-marshes, Saskatchewan

During the 1984 and 1985 summer seasons, we found and collected plants of the Seaside Plantain, *Plantago maritima* L., at two separate locations in the lower Carrot River valley of east-central Saskatchewan. This species is reported here as new to the flora of Saskatchewan. Our first collection was on the broad, saline, marshy flats about 0.7 km south of the Nitenai River, about 2.5 km south of the Carrot River, and north of Highway no. 55 (The Kelsey Trail) about 7 km west of its junction with Highway no. 9, about 85 km north of Hudson Bay Junction (c Sec. 22, T 53 N, R 02 W 2nd M; 53° 35′ 25″N, 102° 13′W; 17 July 1984, *no. 32767*). The plants were locally abundant on the marshy borders of salt-spring pools where they were closely associated with *Triglochin maritima* L. Our second collection was on the extensive saline, marshy flats just southeast of Shoal Lake, about 0.5 km west of Pakwaw Lake village, on the Shoal Lake Indian Reserve, about 100 km east of Nipawin (ne Sec. 10, T 52 N, R 05 W 2nd M; 53° 28′ 45″N, 102° 39′ W; 18 July 1984, *no. 32837*). The plants occurred in a similar habitat to those at the previous location, being limited to the very edges of salt-spring pools. They were locally frequent with *Triglochin maritima,* the only immediate associate, with the exception of some scattered *Scirpus validus* plants that were more or less emergent just off the pond edges.

Plantago maritima sensu lat. (including *P. juncoides* Lam., *P. decipiens* Barneoud, *P. borealis* Lange, *P. oliganthos* Roemer &

Schultes, and *P. glauca* Hornem.) is a circumboreal and bipolar, primarily sea-coast species which in North America reportedly occurs along the Pacific Coast (Aleutian Islands and southern Alaska, south to southern California), the Atlantic Coast (Greenland, southern Baffin Island and Labrador, south to New Jersey), and along the shores of the Hudson, James, and Ungava Bays (Hultén, 1949, 1968; Fernald, 1950; Gleason, 1952; Bassett, 1973; Hitchcock et al., 1959; Scoggan, 1979; Porsild & Cody, 1980). It is apparently absent on the North American Arctic Coast except for a single reported station on the Mackenzie River delta (Hultén, 1968; Scoggan, 1979) which, however, was omitted by Cody (1979) and Porsild & Cody (1980). (Figure 1). The characteristic seacoast habitats for the species are moist, saline sand-beaches, rock-ledges and tidal marshes.

In addition to its maritime coastal distribution indicated above, *Plantago maritima* has also been recorded at the following, quite widely separated stations in the continental interior: CANADA: **Yukon Territory:** Kluane National Park, in "alkaline pools" (Doug-

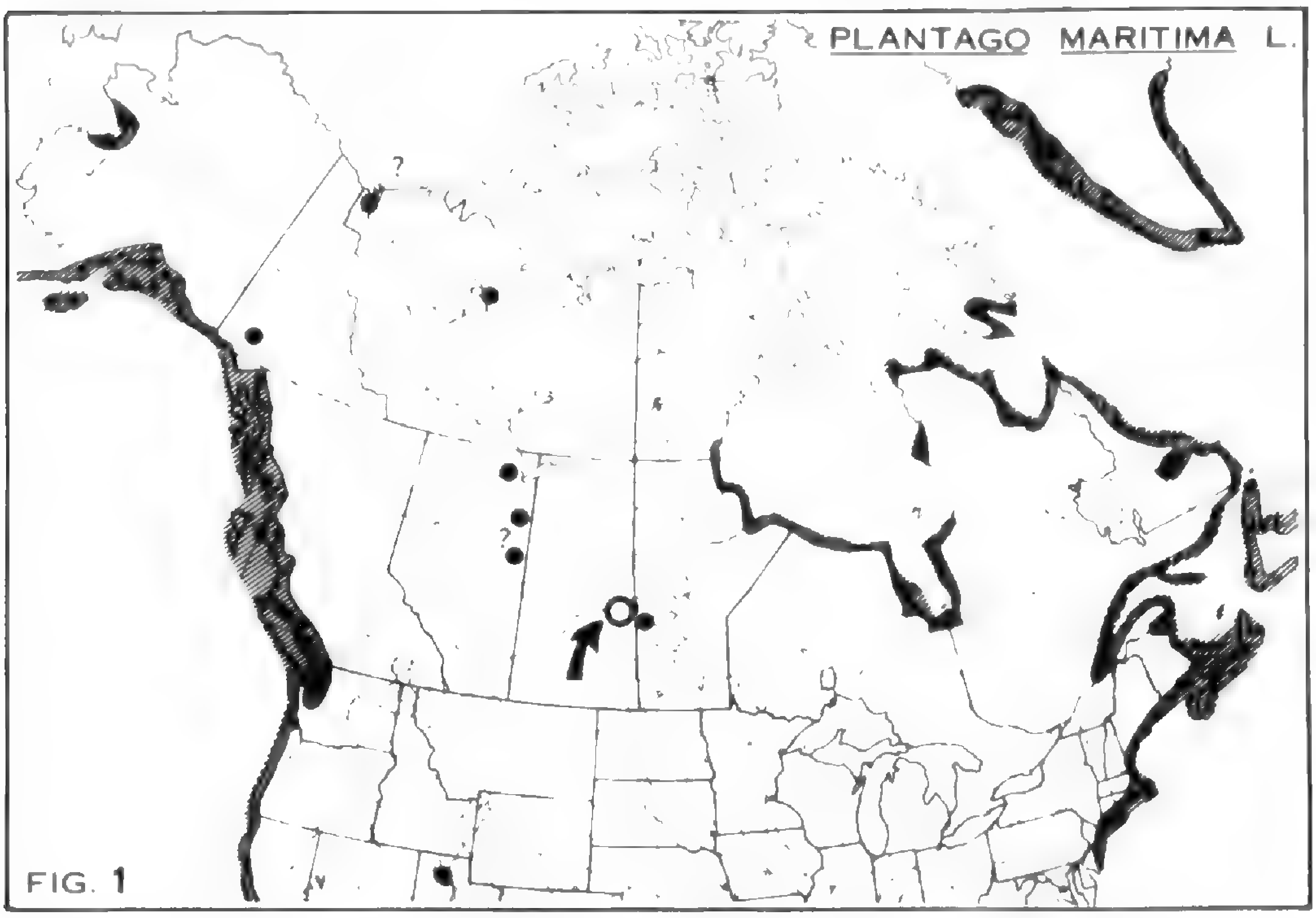

Figure 1. Recorded distribution of *Plantago maritima* in North America. Hatching indicates the maritime coastal distribution; closed dots include the isolated and continental interior stations; open circle and arrow indicate the newly reported Saskatchewan sites.

las, 1974; Douglas et al., 1981). **District of MacKenzie, Northwest Territories:** north shore of McTavish Bay of Great Bear Lake, at "saline springs" (Cody, 1979; Scoggan, 1979; Porsild & Cody, 1980). **Alberta:** Wood Buffalo National Park, on "saline soil" (Argus & White, 1978; Scoggan, 1979) or in "saline marshes" (Packer, 1983; Packer & Bradley, 1984). Boivin (1972) listed it also from "Heart Lake," presumably this being in east-central Alberta, northeast of Lac la Biche, at 55° 02′ N, 111° 30′ W. Packer & Bradley (1984) further mapped the species at a lower Clearwater River site (56° 41′ N, 110° 46′ W) in northeastern Alberta, based on a collection by Peter Lee on 28 June 1983 from "saline marshes" (J. Packer, pers. corr. 26 Oct. 1984). Scoggan (1979) also lists *Plantago maritima* for Alberta from "saline soil along the Red Deer River, Alberta, where taken by John Macoun in 1881." But the latter appears erroneously referred by Scoggan to the Red Deer River in Alberta rather than to the river of the same name in west-central Manitoba, as seems clearly indicated by Macoun's (1884, p. 393) own citation: "in great profusion in and around salt marshes on Red Deer River about one mile from Lake Winnipegosis, Lat. 53° (*Macoun*)." **Manitoba:** Dawson Bay of Lake Winnipegosis and Red Deer River above mouth, at "salt springs," in "salt marshes," or on "saline" or "alkaline soils" (Macoun, 1884; Scoggan, 1957; Boivin, 1972; Scoggan, 1979; White & Johnson, 1980). A report by Lowe (1943) of "*P. decipiens*" as rare on "sea beaches and alkaline areas" on the "Old Souris channel s. of Melita" in Manitoba, was apparently discounted by Scoggan (1953, 1957) as presumably based on misidentified *P. elongata.* U.S.A.: **Utah:** Great Salt Lake (Hitchcock et al., 1959; Scoggan, 1979).

Our newly reported Carrot River valley populations of *Plantago maritima* from along saline spring pool edges in the lower Carrot River valley add to the foregoing list of inland stations, and are the first records for Saskatchewan. They are located approximately 110 and 125 km, respectively, northwest of the interior Manitoba station at Dawson Bay—Lower Red Deer River, where the species was first collected over a century ago by John Macoun.

In the Canadian Prairie Provinces, the species most similar to *Plantago maritima,* at least in general appearance, is probably *P. elongata* Pursh (including *P. pusilla* auct., *non* Nutt.). But *P. elongata* consists of smaller (mostly <10 cm high), more delicate, slender-stemmed, annual plants with slender taproots, in contrast to our mostly larger, coarser, perennial *P. maritima* plants with thickish roots and usually branched caudices. Also our *P. maritima* plants, in contrast to those of *P. elongata,* have (1) leaves fleshy (rather than non-fleshy), (2) corolla tubes short-villous (rather than glabrous), (3) corolla lobes spreading and over 1 mm long (rather than often erect and less than 1 mm long), (4) anthers 4 (rather than 2), (5) spike axis distinctly short-pubescent (rather than glabrous), and (6) flowering and fruiting spikes thicker and denser (rather than slender and loosely flowered).

The New World populations of *Plantago maritima* appear best accepted as subsp. *juncoides* (Lam.) Hultén, separable from the Eurasian subsp. *maritima* on the basis of their broader bracts and more numerous ovules (Hitchcock et al., 1959; Bassett, 1973). Further varietal segregates have often been distinguished within North American populations (Fernald, 1925, 1950), but also frequently questioned as being perhaps merely environmental forms (Rousseau, 1942; Gleason, 1952; Hitchcock, 1959). Our collected sample of 38 Saskatchewan plant specimens can be characterized as follows: (1) leaves entire, stiffishly erect, (1–) 1.5–3 (–4) mm wide, (7–) 10–20 cm long, mostly somewhat shorter than the spike-bearing scapes; (2) spike-bearing scapes 10–23 cm high, strictly erect or often somewhat curved above; (3) spikes 1–10 cm long, densely compact or flowers somewhat separated below; (4) bracts mostly distinctly keeled, the tips not prolonged, and the margins glabrous to usually slightly or sometimes distinctly ciliolate; (5) calyx-segment margins glabrous or often remotely ciliolate; (6) seeds oblongish, 1.3–2.5 mm long; and (7) anthers 1–1.5 mm long, with their "subulate-tips" about 0.25 mm long. Upon application of the taxonomic criteria given by Fernald (1925, 1950), most of our material would be identified as his *P. juncoides* var. *decipiens* (Barneoud) Fern., although some characters of his *P. oliganthos* R. & S. are frequently present (e.g., bracts distinctly keeled, they and the calyx-segments often glabrous or only remotely ciliolate). A few of the smaller plants with shorter spikes might well be individually identifiable as *P. juncoides* var. *glauca* (Horneman) Fern., although they clearly belong within the same local populations from which our sample was collected. While the Saskatchewan collections represent a basis too limited for taxonomic conclusions, their populational variation at least suggests the probable presence of only weak distinctions, if any, between the "forms" represented by the epithets: *decipiens, glauca,* and *oliganthos.* But even if these three "taxa" were to be merged under a broader *P. maritima* var. *glauca* Horneman (the epithet among these three with priority at the varietal rank), taxonomic questions would still remain regarding its separation from the more western *P. maritima* var. *juncoides* (Lam.) Gray and var. *californica* (Fern.) Piper, and the more eastern taxon that has often been recognized as *P. juncoides* var. *laurentiana* Fern. These taxonomic questions are beyond the scope of this paper.

During the 1985 summer, within the broad Nitenai River salt marsh, our first collecting site for *Plantago maritima,* we also discovered and collected plants of *Carex mackenziei* Krecz. as new to the flora of Saskatchewan (se Sec. 22, T 53 N, R 02 W 2nd M; 53° 35′ 25″ N, 102° 13′ W; 24 June 1985, *no. 33,803*). The plants occurred on wet, somewhat raised, hummocky, salt-spring mounds (in contrast to salt-spring pool edges where *Plantago maritima* was found). Despite a relatively extensive although hardly thorough search of the broad, over 150-hectare marsh, only a single relatively limited local population consisting of about 100 plants was found, contained within an area of less than 100 m^2. The other plant species most closely associated with this sedge were *Triglochin maritima* L. *Scirpus rufus* (Huds.) Schrad., and *Glaux maritima* L.

Carex mackenziei is a circumpolar maritime species, characteristic of tidal and other saline marshes. In North America it reportedly occurs in Alaska along the Arctic, Bering and Pacific coasts from Kotzebue Sound south to Sitka (Hultén, 1968), at the Mackenzie River delta in the Northwest Territories on the Arctic coast (Hultén, 1968; Porsild & Cody, 1980), along the Hudson Bay and James Bay coasts from southern Keewatin District to the Great Whale River in Quebec, and along the Atlantic and Gulf of St. Lawrence coasts from Labrador, south to Nova Scotia and Maine (Fernald, 1950; Gleason, 1952; Hultén, 1968; Scoggan, 1978; Porsild & Cody, 1980). Our present Saskatchewan report of *Carex mackenziei* is particularly significant since it apparently represents the first known record for the species from the continental interior of North America. (Figure 2).

With regard to the newly reported Saskatchewan occurrences of two characteristically maritime coastal salt marsh species, it may be

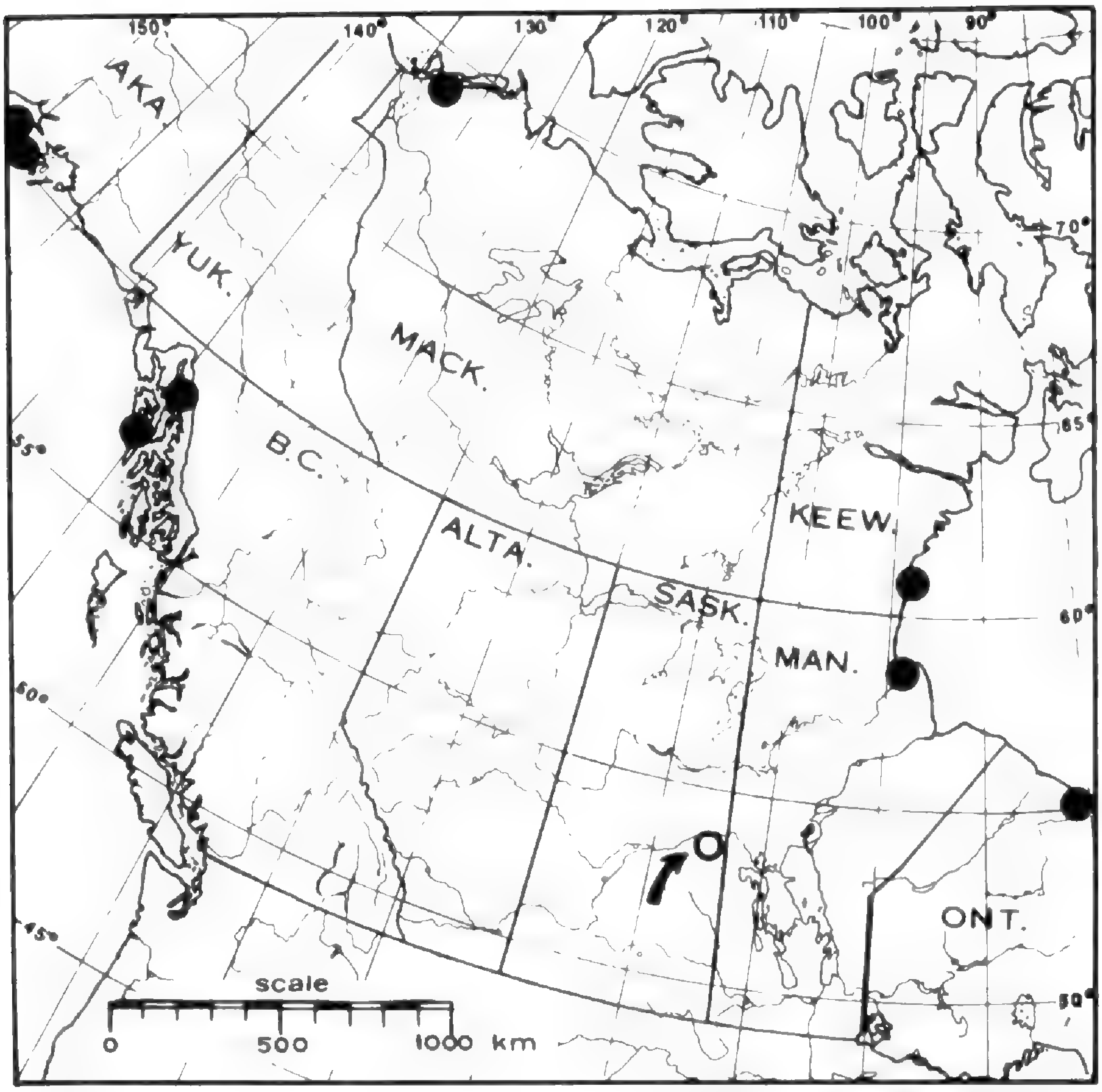

FIG. 2 CAREX MACKENZIEI

Figure 2. Recorded distribution of *Carex mackenziei* in Western Canada. Closed dots indicate the previously reported localities; the open circle and arrow indicate the newly reported Saskatchewan site.

significant that the salinity of the pertinent Carrot River Valley salt springs and marshes in which these species were found is mainly due to their sodium chloride content rather than the sodium sulfate that is characteristic of most Saskatchewan saline lakes and marshes.

The occurrences of maritime coastal salt marsh species such as *Plantago maritima* and *Carex mackenziei* in the continental interior of Western Canada as rarities at widely spaced isolated outposts pose an interesting, albeit difficult, phytogeographical question with respect to how such distributional patterns were originally attained. A post-Pleistocene marine incursion extensive enough to account for such distributions is hardly a viable postulate. We would hypothesize that such seacoast species likely spread along semi-open receding shores of the large and perhaps at times estuarian-like post-glacial Lakes Agassiz and McConnell, especially during their latter stages (about 5000–4000 years ago) when connections or near-connections existed to Hudson Bay and the Arctic Ocean, respectively. Subsequent survival would then have occurred only at a few persistent, favorable interior sites, which in the cases of *P. maritima* and *C. mackenziei* appear to have been mainly sodium chloride salt-springs within saline marshes.

Plantago maritima was accorded rarity status for the Yukon (Douglas et al., 1981), the continental Northwest Territories (Cody, 1979), Alberta (Argus & White, 1978; Packer & Bradley, 1984), Manitoba (White & Johnson, 1980), and Ontario (Argus & White, 1977). *Carex mackenziei* was accorded rarity status for the continental Northwest Territories (Cody, 1979) and Manitoba (White & Johnson, 1980). Both species now deserve a similarly rare status for Saskatchewan as well.

The collections cited in this paper are those of the authors, with voucher specimens deposited at SASK and USAS. Duplicates will also be filed in DAO and CAN.

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V. L. H.
THE W. P. FRASER HERBARIUM
UNIVERSITY OF SASKATCHEWAN
SASKATOON, SASKATCHEWAN
CANADA S7N 0W0

D. F. H.
BOX 40
SOMME, SASKATCHEWAN
CANADA S0E 1N0

L. B.
BOX 90
CARRAGANA, SASKATCHEWAN
CANADA S0E 0K0

DISPERSION PATTERN OF AERIAL SHOOTS OF THE COMMON MARSH REED *PHRAGMITES AUSTRALIS* (POACEAE)

ANDREW N. DAVIS AND TIMOTHY L. BRIGGS

ABSTRACT

The dispersion pattern of aerial shoots of the common marsh reed, *Phragmites australis* (Cav.) Trin. ex Steud., was determined by density counts from a marsh population in southeastern Massachusetts using quadrat methods. Statistical analyses of 0.0625 m^2 quadrat data indicated a random dispersion pattern. An aggregated dispersion pattern is indicated by analyses of 0.25 m^2 quadrat data. The aggregated dispersion pattern appears to be a reproductive pattern based on the mode of population development of *P. australis* in which extensive vegetative propagation forms aggregations of aerial shoots. In addition, the number of shoots per aggregate exhibited a logarithmic distribution that conforms to the concept of a viable unit.

Key Words: *Phragmites australis,* dispersion pattern, marsh reed, aerial shoots, ecology, southeastern Massachusetts

INTRODUCTION

The common marsh reed, *Phragmites australis* (Cav.) Trin. ex Steud. [= *P. communis* Trin. (Clayton, 1968)] may be the most widely distributed angiosperm in the world, growing in fresh or brackish waters in pure or nearly pure stands. This species has been found in strata that date back to the Miocene (Tertiary Period) (de la Cruz, 1978), and is believed to have evolved in subtropical regions from where it subsequently spread to temperate areas in both hemispheres. Its present distribution ranges from Norway and Canada in the north to southern temperate areas in Australia, Africa, and South America (Haslam, 1972; Holm et al., 1977).

Phragmites australis is a perennial grass with annual aerial shoots that terminate in a distinctive feather-like flower cluster. Although seed set is annual, most are inviable, making establishment from seed rare (Harris and Marshall, 1960; Haslam, 1971a, 1971b, 1972). Meiotic disturbance, flower infertility, pollen lethality, self-incompatibility, inflorescence density, and unfavorable weather during flowering and seed setting, may all lower the percentage of viable fruits produced (Haslam, 1972), as also may clonal and habitat differences. Even with viable seeds, field germination is often poor, and seedlings have rarely been reported (Harris and Marshall, 1960; Haslam, 1972). In addition, young seedlings may be killed by frost, high salinity, flooding, desiccation, or competition (Haslam, 1972).

Phragmites australis also reproduces asexually via vegetative propagules and long-lived rhizomes. The possible range of suitable habitats for seed germination is significantly narrower than that which allows vegetative propagation; e.g., seeds will not germinate in 5 cm of water, yet rhizomes grow and spread in 1 m of water (Haslam, 1972; Holm et al., 1977). The reported infrequent occurrence of seedlings in nature and the extensive vegetative propagation exhibited by *P. australis* led us to investigate the dispersion pattern of this species in a single marsh population. Biological and physical factors that may influence the spatial distribution and density of aerial shoots are considered.

PROCEDURE

Field Methods

Density counts of aerial shoots of *Phragmites australis* in Demarest-Lloyd Memorial State Park, South Dartmouth, Massachusetts (approx. 70°59′17″W, 41°31′40″N) were made March 20, 1984, prior to the emergence of new growth. The *P. australis* stand is in a brackish marsh adjacent to Georges Pond, approximately 175 m along the south side of the state park access road. In order to minimize the effects of environmental heterogeneity on our data, sampling was confined to a 5 m-wide band parallel to and ca. 10 m from a freshwater runoff culvert. Twenty-five 0.0625 m^2 and twenty-five 0.25 m^2 quadrat counts were taken randomly. Only shoots attached to rhizomes were counted in order to minimize the possibility of sampling shoots formed prior to the 1983 growing season. Possible implications of this are addressed below.

Statistical Analyses

The Index of Dispersion was used to test the null hypothesis that *Phragmites australis* shoots are distributed randomly (Greig-Smith, 1964). Data that agreed with this null hypothesis were analyzed by the Chi-square goodness of fit test to verify the fit to a standard Poisson (random) distribution (Greig-Smith, 1964).

Data from the quadrat size that deviated significantly from a Poisson distribution and indicated aggregation were tested for agreement with the negative binomial distribution. Both a Chi-square goodness of fit test (Bliss and Fisher, 1953) and Anscombe's third moments test (Anscombe, 1950) were used.

RESULTS

Field density counts of *Phragmites australis* shoots are presented in Table 1. The results from the Index of Dispersion test indicate that the dispersion pattern of 0.0625 m^2 quadrat data did not deviate significantly from a Poisson distribution (Table 2). The Chi-square goodness of fit test confirms a Poisson distribution for the 0.0625 m^2 quadrat data ($.70 > p > .50$). The Index of Dispersion test shows that the deviation from the random model is highly significant for the 0.25 m^2 quadrat data ($p < .001$), indicating an aggregated distribution (Table 2). The Chi-square goodness of fit test for 0.25 m^2 quadrat data shows no significant difference between observed and expected values in a negative binomial distribution ($.75 > p > .50$). Anscombe's third moments test also indicates that the 0.25 m^2 quadrat data fit a negative binomial distribution ($T = -262.6$ and $2S.E. = 439.2$).

Calculations for statistical analyses are available by request.

Table 1. Field density counts of *Phragmites australis* aerial shoots.

0.0625 m^2 quadrats:	5, 5, 4, 5, 6, 5, 1, 5, 5, 6, 9, 7, 4, 9, 13, 6, 10, 8, 13, 6, 8, 6, 4, 7, 11
0.25 m^2 quadrats:	28, 23, 29, 23, 13, 9, 24, 19, 21, 34, 26, 22, 18, 20, 11, 14, 20, 28, 26, 32, 33, 22, 26, 39, 29

Table 2. Index of Dispersion test for *Phragmites australis* aerial shoot data.

Quadrat	Index of Dispersion					
Size (M^2)	N	$\bar{X}$	S^2	$S^2/\bar{X}$	χ^2(df)	P
0.0625	25	6.72	8.21	1.22	29.30(24)	$.30 > p > .20$(R)
0.25	25	23.56	53.59	2.27	54.60(24)	$p < .001$ (A)**

(R) = random dispersion pattern ($.95 > p > .05$)
(A) = aggregated dispersion pattern ($p \leqslant .05$)
** = highly significant

DISCUSSION

An understanding of dispersion patterns of organisms, i.e. the spacing of individuals with respect to their neighbors, can lead us to causes of their distributions and abundances. The occurrence of any non-random dispersion pattern (aggregated or even) requires outside force or expenditure of energy by the organism. For the latter to occur, the organism must gain some advantage from the pattern. The importance of recognizing the dispersion pattern lies in the correlation of that pattern with biological and physical factors in order to understand the ecology of the species. Causes of distribution patterns within populations may be vectorial, reproductive, social, coactive, or stochastic (Hutchinson, 1953), but are not necessarily mutually exclusive, as several may operate together or succeed one another in time.

In our study, it was determined that aerial shoots of *Phragmites australis* are distributed in an aggregated pattern at the 0.25 m^2 quadrat size. Gorham and Pearsall (1956) noted "a good deal of aggregation in *Phragmites*," but fail to document this observation or suggest possible mechanisms leading to the aggregation.

The mode of vegetative reproduction of *Phragmites australis* can be correlated with the aggregated distribution of the species. Population development within an established area occurs primarily by proliferation of underground rhizomes leading to extensive clones, some of which may persist for hundreds of years (Haslam, 1971a, 1972). Horizontal rhizomes that reach 2–3 m in length (Holm et al., 1977), branch to form other horizontal rhizomes and initiate vertical rhizomes (Haslam, 1970, 1972). Aerial shoots are produced from buds near the growing tips of the vertical rhizomes. The shoots emerge in a "bunched arrangement" (Haslam, 1970) that can account for the aggregated dispersion pattern observed. Factors influencing underground portions of *P. australis* plants are unknown, but may also be important in determing the aggregated dispersion pattern of shoots.

The aggregated dispersion of *Phragmites australis* shoots fits the negative binomial distribution; the clumps are randomly spaced but the number of individual shoots per clump exhibit a logarithmic distribution. Thus, the presence of one aerial shoot increases the probability that others will be there. Haslam (1971b) suggested a viable unit of ca. 10 shoots per seedling for British populations of *P. australis*. It is not until this stage that a sedling develops a stressresistant horizontal rhizome (Haslam, 1971b). When a number of shoots occur together, there is greater possibility for survival under stressful conditions by reorientation of food reserves. The concept of a viable unit for a seedling can be extrapolated to the degree of aggregation of aerial shoots produced annually from a vertical rhizome, and may explain the negative binomial distribution of the aggregated shoots in our study. The mean number of shoots at aggregation was 23.56, indicating a larger viable unit for our population in comparison with British populations as noted above (Haslam, 1971b). Physical factors [floods, drought, nutrients, light, temperature, and salinity (Haslam, 1970, 1971a, 1971b, 1972)] and biological factors [competition and herbivory (Haslam, 1970, 1971b)] may influence the density of aerial shoots and size of clumps. The concept of a viable unit warrants further research and, along with the mode of vegetative reproduction, may explain the aggregated distribution of aerial shoots and the degree to which it occurs.

We recognize that the observed aggregated dispersion pattern for *Phragmites australis* shoots may be a transient pattern at this stage in the development of the population. Maturation of the *P. australis* stand may result in changes in the dispersion pattern. Also, another dispersion pattern may have been masked if more than one year class of shoots were sampled. In dense populations in Britain, some shoots may remain standing for up to 2 seasons, with older shoots becoming brittle (Haslam, 1972). However, we counted only shoots attached to rhizomes, and the winter conditions at our site may preclude older, brittle shoots staying attached to their rhizomes through two winters.

In summary, aerial shoots of *Phragmites australis* are distributed in an aggregated manner and according to the negative binomial. This distribution appears to be a reproductive pattern based on the mode of vegetative propagation. Biological and physical factors may be involved in determining density of aerial shoots and size of the clumps. Degree of aggregation may be a response to environmental stresses, and conforms to the concept of a viable unit. Biological implications of the vegetative mode of development for stands of this species are evident in the widespread distribution and success of *P. australis.*

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DEPARTMENT OF BOTANY
UNIVERSITY OF MASSACHUSETTS
AMHERST, MASSACHUSETTS 01003

SEASONAL SUCCESSION AND VERTICAL DISTRIBUTION OF PHYTOPLANKTON IN CANDLEWOOD LAKE, CT

Stanley J. Freeda[1] and Peter A. Siver

ABSTRACT

Preliminary to development of a management plan for Candlewood Lake (Fairfield and Litchfield Counties, CT), phytoplankton populations were recorded at several sites from April, 1983 through January, 1984. Vertical phytoplankton profiles were identified and counted to derive seasonal succession patterns and population concentrations. Vertical profiles of nitrate, phosphorus, chlorophyll a, phaeophytin a, temperature, conductivity, dissolved oxygen, and light were also recorded at the sampling sites. Distributions of phytoplankton were seasonal; approximately 10^4 cells/ml occurred in the epilimnion during summer stratification. The lake was dominated (89%) by blue-green algae (Oscillatoriaceae and Nostocaceae). Diatoms and green algae were important during spring and winter, respectively. Horizontal phytoplankton distributions throughout the lake were similar and correlated well with chlorophyll a concentrations. Nitrate concentrations were generally low (< 0.3 mg NO_3/l) to non-detectable during the summer. Total phosphorus was found to be high, averaging 35 μg/l on the surface. Candlewood Lake is thus in an early eutrophic state.

Key Words: phytoplankton, eutrophication, seasonal succession, nitrate, phosphate, western Connecticut

INTRODUCTION

Candlewood Lake (Fairfield and Litchfield Counties), the largest lake in Connecticut, covers 2194 hectares and has 105 km of shoreline. Over the past decade, this lake experienced accelerated eutrophication. In the early 1970's, it was classified as early mesotrophic (Norvell and Frink, 1975). By the late 1970's, phosphorus levels had doubled and the lake was classified as mid to late mesotrophic (DEP, 1983). In 1983, phosphorus concentrations were sufficient to classify sections of the lake as eutrophic (Siver, 1984).

In addition to increased phosphorus levels, major changes in aquatic vascular plant populations have occurred since 1979. *Myriophyllum spicatum* L. has become the major dominant aquatic vascular plant (Siver, 1984), and its heavy growth has greatly impeded

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[1] Present Address: Department of Botany and Plant Pathology, University of New Hampshire, Durham, NH 03824.

recreational activities on Candlewood Lake, a major economic and recreational resource in western Connecticut.

In general, algal populations are not a major problem, although dense blooms have been reported in isolated bays. Lake management programs aimed at controlling weed growth such as aquatic plant population controls by herbicides and lake drawdowns are under consideration. Baseline information is relevant prior to the proposed management practices, to answer the question to what extent such management practices would affect lake phytoplankton. The present study was conducted in order to determine distribution of phytoplankton in Candlewood Lake in relation to its present physical and chemical parameters.

MATERIALS AND METHODS

Phytoplankton Enumerations

Vertical quantifications of phytoplankton populations were made in Danbury Bay (Site 1) at 1.0 m intervals from April through November, 1983, and in January, 1984. During April, May and August, similar vertical profiles were taken from New Fairfield Bay (Site 2) and Lattin's Cove (Site 3) (Figure 1). In May and August, epilimnetic samples were taken from three additional sites for comparative purposes: Pocono Point (Site 4), Orchard Point (Site 5) and Chatterton Point (Site 6).

All samples were collected using a horizontally positioned van Dorn bottle and were fixed with Lugol's Solution (Franson, 1980); phytoplankton were identified and counted at 600× with an inverted microscope using settling chambers constructed with the slight modifications of Coulon and Alexander (1972). Time periods required to settle all cells completely in the sample volume ranged from 24 to 48 hours (Furet and Benson-Evans, 1982). Counts were made along horizontal transects across the diameter of the settling chamber. Because the top ten taxa accounted for 95% to 99% of the total cell concentration in each sample, they were used to calculate the composition of phytoplankton in each algal class.

Chemical and Physical Parameter Enumerations

Water samples for chlorophyll analysis were taken bimonthly during the summer and monthly during autumn and winter at vertical meter intervals from sites 1 to 3. Samples at sites 4 to 6 were taken at 1 m and from an equal mix of the top seven meters of

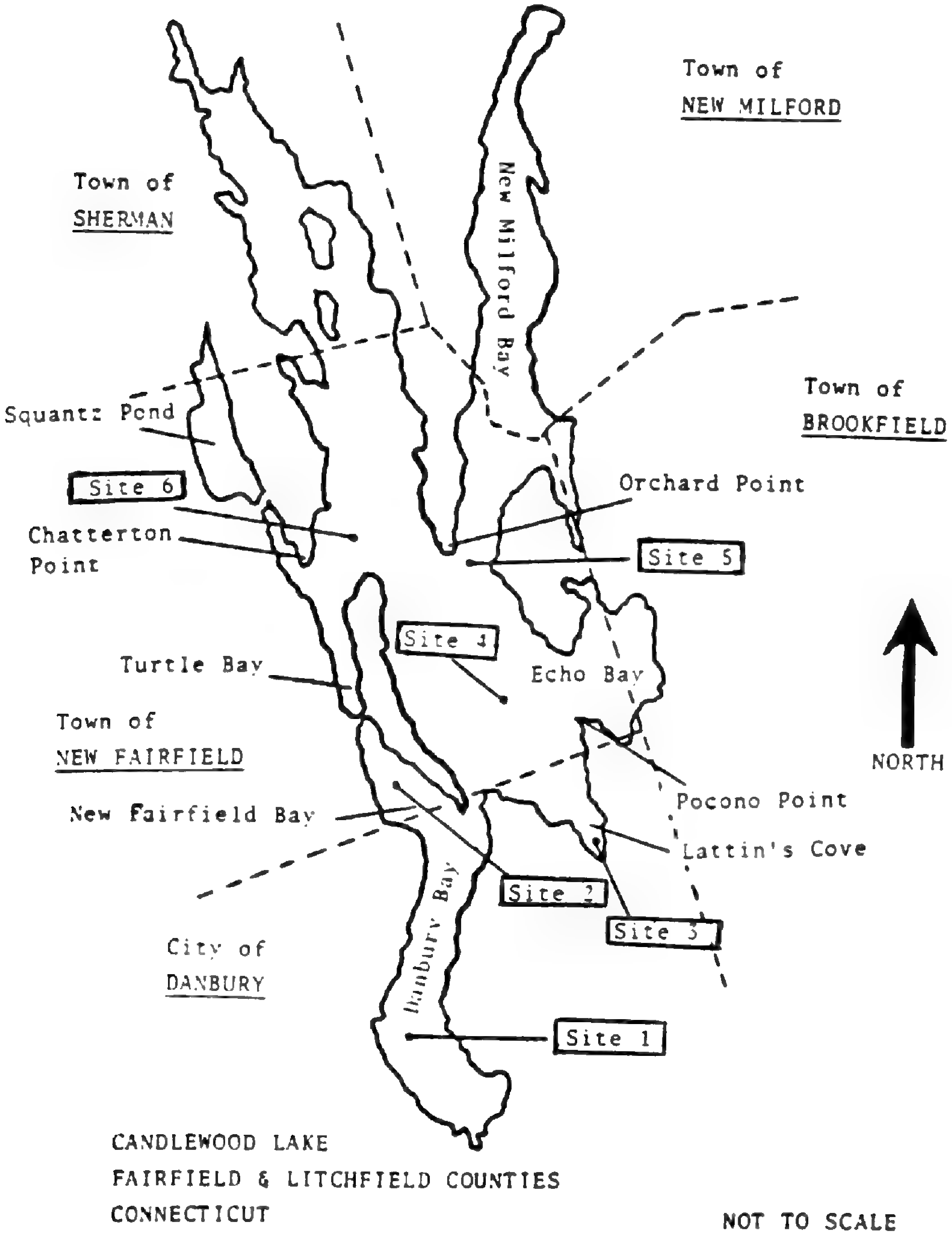

Figure 1. Map of Candlewood Lake (Fairfield and Litchfield Counties, CT) showing locations of the towns, major bays, and the six study sites. Drawing not to scale.

epilimnetic water. From 200 to 1000 ml of sample were passed through glass fibre filters buffered with 0.2 ml of saturated magnesium carbonate ($MgCO_3$) suspension. Chlorophylls were extracted with 90% acetone using a power tissue grinder, the suspension was centrifuged at 2000 rpm for 10 min, and concentrations of chlorophylls a, b, and c were determined using the trichromatic method (Franson, 1980). Because chlorophyll a may be overestimated by breakdown products such as phaeophytin a, another method was used to estimate the chlorophyll a and phaeophytin a levels (Lorenzen, 1967).

Nitrate concentrations were determined by reducing the nitrate to nitrite using cadmium reduction. The nitrite level was measured spectrophotometrically by diazotizing with sulfanilamide and coupling with N-(1-napthyl)-ethylenediamine (NED) to form a violet azo dye (Franson, 1980). Each 75 ml sample was first passed through a glass fibre filter, mixed with 25 ml of NH_4Cl-EDTA, and allowed to flow through the cadmium reduction column (modified from Eppley, 1978). The first 50 ml were discarded and the remainder used for nitrate determinations; columns were rinsed between samples with 40 ml of dilute NH_4Cl-EDTA.

Total phosphorus was determined after acid persulfate digestion of non-filtered water samples using the stannous chloride method (Franson, 1980); pH was determined using a Fisher model 750 pH/ion meter.

At each site, vertical profiles of conductivity, dissolved oxygen, and light levels were determined; the Secchi disk depth was also recorded. Temperature and conductivity were measured using a YSI model 33 temperature/conductivity meter; light was measured with a Licor Li-185 B Quantum Sensor Photometer, and dissolved oxygen was measured using a YSI model 58 Dissolved Oxygen meter that was standardized by the Winkler titration method (Franson, 1980).

RESULTS

Phytoplankton

During the study, phytoplankton concentrations ranged from a low of 2.9×10^3 cells/ml in January to a high of 1.3×10^5 cells/ml in August. In Danbury Bay, mean concentrations increased from 1.5×10^4 cells/ml in April to the seasonal maximum of 5.43×10^4 cells/ml in August, and then gradually decreased to a seasonal minimum of 8.27×10^3 cells/ml during January (Figure 6).

Vertical distributions of phytoplankton numbers in Danbury Bay were uniform from April through June, ranging from 0.5 to 3.0 ×

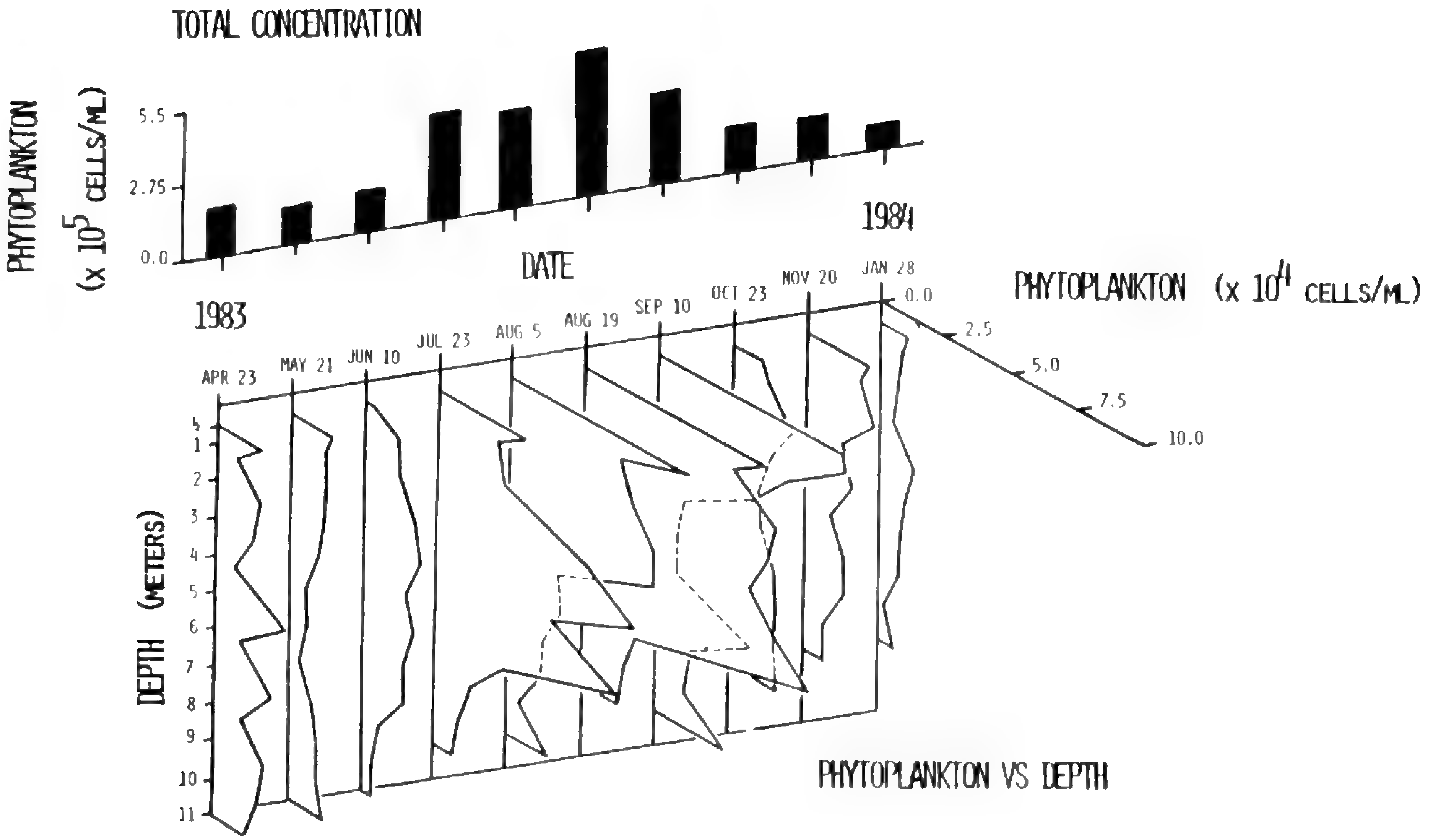

Figure 6. Phytoplankton concentration versus depth and time in Danbury Bay (Site 1), Candlewood Lake, CT. The sum of the concentrations at each depth is represented by the bars above each profile.

10^4 cells/ml (Figure 6). As the summer progressed, large epilimnetic populations developed, with a maximum of 8.5×10^4 cells/ml at 6 m on August 19. Vertical distributions were again uniform during October, November and Janaury.

The phytoplankton taxa in Danbury Bay were similar throughout the study, but varied in concentration and, therefore, dominance. Overall, Cyanophyceae represented 89% of the total cells in the bay during the study. On a monthly basis, Cyanophyceae accounted for over 68% of the total flora each month, except during January, at which time they comprised 49% of the phytoplankton community (Figure 7). The Bacillariophyceae were most abundant in the spring (31% in April), and decreased to insignificant levels by June. The Chlorophyceae and Cryptophyceae were most important during autumn and winter (Figure 7).

Phytoplankton concentrations were similar at all sites (Figure 8). For example, in May the mean phytoplankton numbers were low at all sites, ranging from 5.28×10^3 to 1.43×10^4 cells/ml. During August, all sites had mean epilimnetic phytoplankton levels between 3.86×10^4 to 1.18×10^5 cells/ml.

Phytoplankton community structure was similar at all six sites during May and August (Table 1). On May 21, at all but the Chatterton Point site, the Cyanophyceae accounted for greater than 88% of the phytoplankton. The dominant taxa were *Oscillatoria Agardhii* Gomont, *O. amphigranulata* van Goor, and *Anabaena laxa* Rabenhorst. During August, the blue-green algae accounted for over 80% of the flora at all six sites, with *O. amphigranulata* and *A. laxa* being the most abundant taxa.

Chemical and Physical Parameters

Temperature profiles at the Candlewood Lake sites denoted a typical, dimictic, temperate lake with a temperature range of 0.9–25.6°C. Conductivity ranged from a winter minimum of 60 μmhos/cm to a summer maximum of 133 μmhos/cm. During most of the study period, pH values were between 7 and 8, except in the hypolimnion during summer anoxic conditions. Saturated levels of dissolved oxygen occurred throughout the lake, except in the hypolimnion and portions of the metalimnion during summer stratification. The light extinction coefficient, η, ranged from 0.67–1.33, increasing as the summer progressed. Light did not penetrate below 7 m on sunny days (when incident light levels were greater than 1500

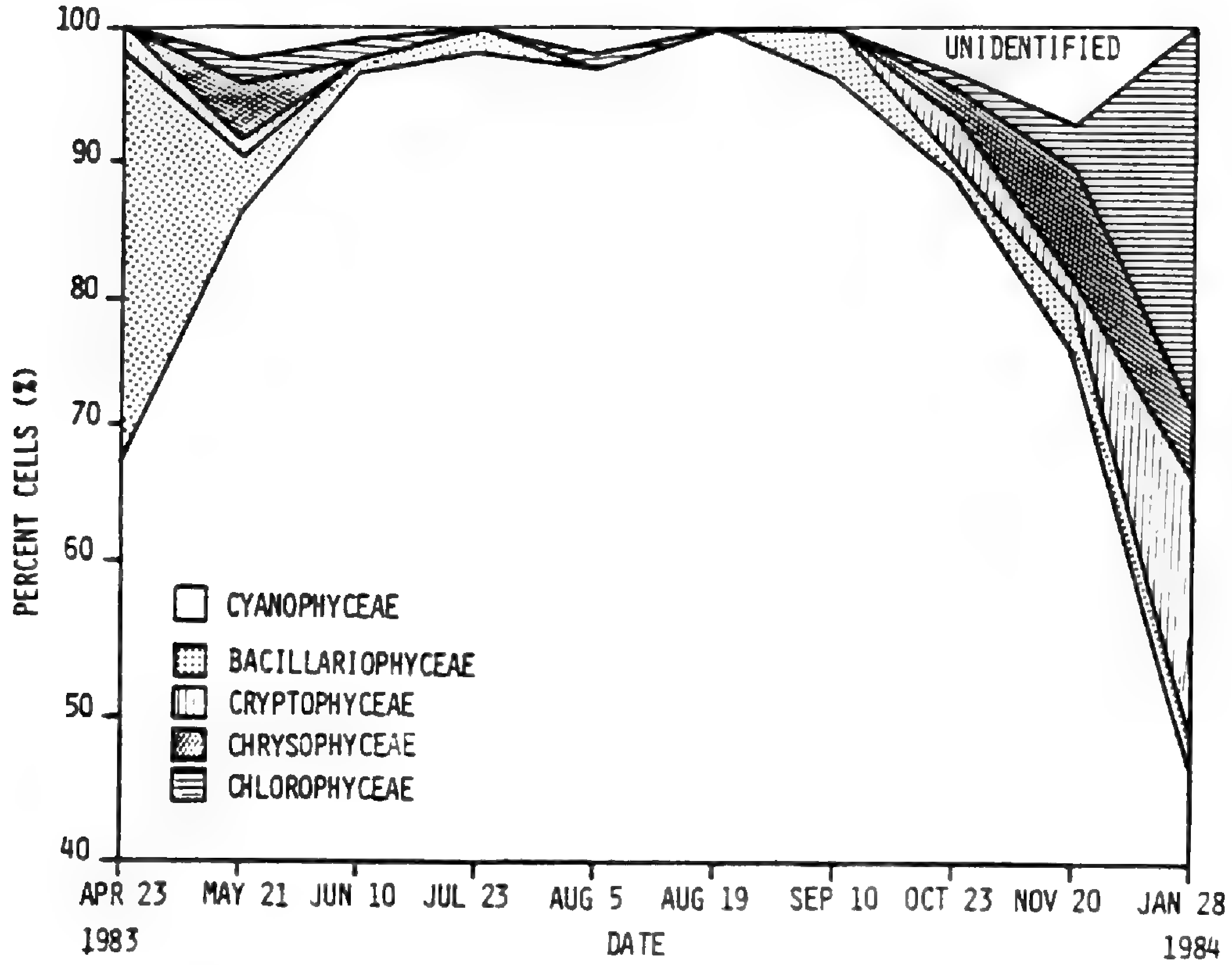

Figure 7. Percentage of phytoplankton per algal class in Danbury Bay (Site 1), Candlewood Lake, CT, April, 1983–January, 1984.

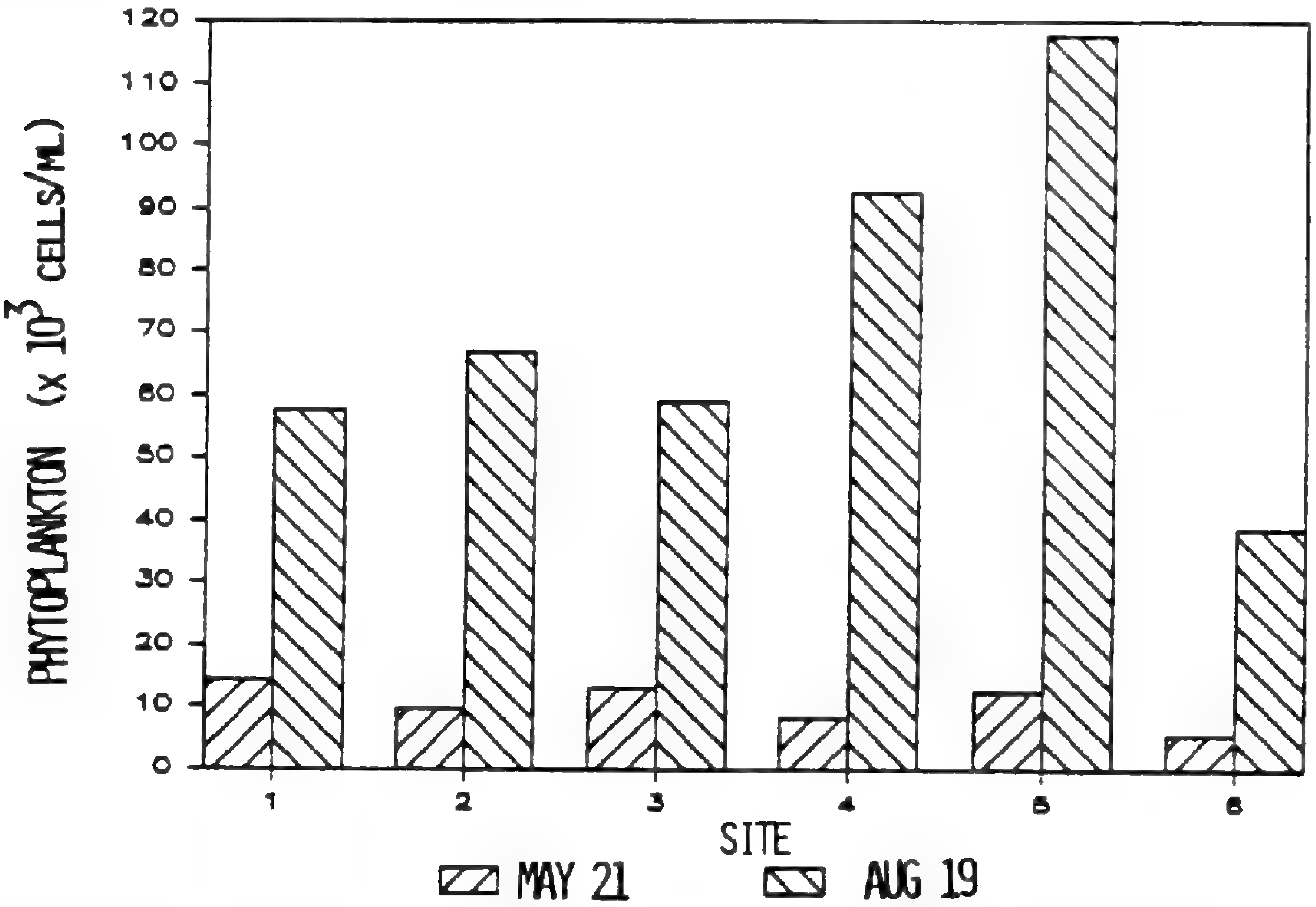

Figure 8. Phytoplankton concentrations at 1 m in Danbury Bay (Site 1); New Fairfield Bay (Site 2); Lattin's Cove (Site 3); Pocono Point (Site 4); Orchard Point (Site 5); and Chatterton Point (Site 6) in Candlewood Lake, CT on May 21 and August 19, 1983.

Table 1. Percentage of total cells belonging to each class found on the sampling dates May 21 and August 19, 1983 at 1 m for the six sampling sites, Candlewood Lake, CT.

Site	Class	Percentage of Total Cells (%) 21 May 1983	 19 August 1983
1	Cyanophyceae	94	100
2	Cyanophyceae	90.3	92.4
	Bacillariophyceae	5.9	
	Chrysophyceae		4.3
3	Cyanophyceae	97	79.7
	Chlorophyceae		18.7
4	Cyanophyceae	88	97
	Bacillariophyceae	6.9	
5	Cyanophyceae	91.9	99.3
	Bacillariophyceae	3.9	
6	Cyanophyceae	65	89
	Bacillariophyceae	21	4.4
	Chrysophyceae		4.4
	Chlorophyceae	6.2	

μE/cm^2), or below 4–5 m on cloudy days (with incident light levels of 40–400 μE/cm^2). The Secchi depth rarely extended below 3 m.

Nitrate concentrations were low at all sites during the study period, ranging from non-detectable levels to 0.262 mg NO_3/l. In Danbury Bay, nitrate concentrations of 0.086 mg NO_3/l were detected during spring overturn (April); however, levels decreased to non-detectable by mid-summer (Figure 2). Nitrate concentrations increased during autumn overturn and reached a seasonal maximum in January.

Total phosphorus in Danbury Bay ranged from 10 to 125 μg/l during the study period (Figure 3). Phosphorus concentrations were often higher in surface waters (0.5 m), decreased slightly with depth to 8 m, and then increased substantially below 8 m. Mean phosphorus levels of surface water and water between 1 and 8 m were 35 and 25 μg/l, respectively. Below 8 m, the mean phosphorus concentration was 55 μg/l.

Chlorophyll a concentrations throughout Candlewood Lake ranged from 0 to 44 mg/m^3, with the greatest concentration of chlorophyll a in the epilimnion during the summer. Lower, more uniform levels were recorded during spring and autumn overturns (e.g., Danbury Bay, Figure 4). The chlorophyll levels corresponded well with phytoplankton concentrations throughout the year (Figure 5). Phaeophytin a levels were generally greatest on the lake bottom and were rarely detected in the epilimnion (Figure 4). Chlorophyll b and c concentrations were non-detectable throughout most of the year, especially in the summer. Peaks of 2.74 and 0.54 mg/m^3 for chlorophyll c and b, respectively, occurred during January.

DISCUSSION

Over the past five years, Candlewood Lake has experienced change, probably the result of cultural eutrophication. Phosphorus levels in Candlewood Lake during the early 1970's were indicative of an early mesotrophic condition (Frink, 1971; Norvell and Frink, 1975). By 1980, average phosphorus concentrations had increased to the point where the lake was considered mid-mesotrophic (DEP, 1983). During 1983, mean phosphorus levels in Danbury and New Fairfield Bays were 75% and 35% greater, respectively, than in 1980–81 (Siver, 1984). The rapid rise in the lake's phosphorus concentration was probably due to a combination of factors associated with cultural eutrophication (e.g., failing septic systems, increased runoff, fertilizers) and with loading from the sediments. Further research will be necessary to determine the relative importance of each contributing factor.

Major changes in both species and densities of aquatic vascular plants have occurred since 1979 within the lake (DEP, 1983; Siver, 1984). *Ceratophyllum sp., Vallisneria americana* Michx., and *Potamogeton spp.* were dominant forms in many areas of the lake during 1979 (DEP, 1983); however, by 1983 *Myriophyllum spicatum* L. was by far the most abundant aquatic macrophyte throughout the lake.

Concurrent with enhanced nutrients and aquatic weeds has been a further shift toward domination of the phytoplankton community by the Cyanophyceae. Although blue-green algae dominated the lake's phytoplankton community during the late 1970's and early 1980's, Chlorophyceae and Bacillariophyceae were also common (DEP, 1983). Phytoplankton analysis prior to the present study included only surface samples. In the present study, including vertical analyses of phytoplankton concentrations throughout the year,

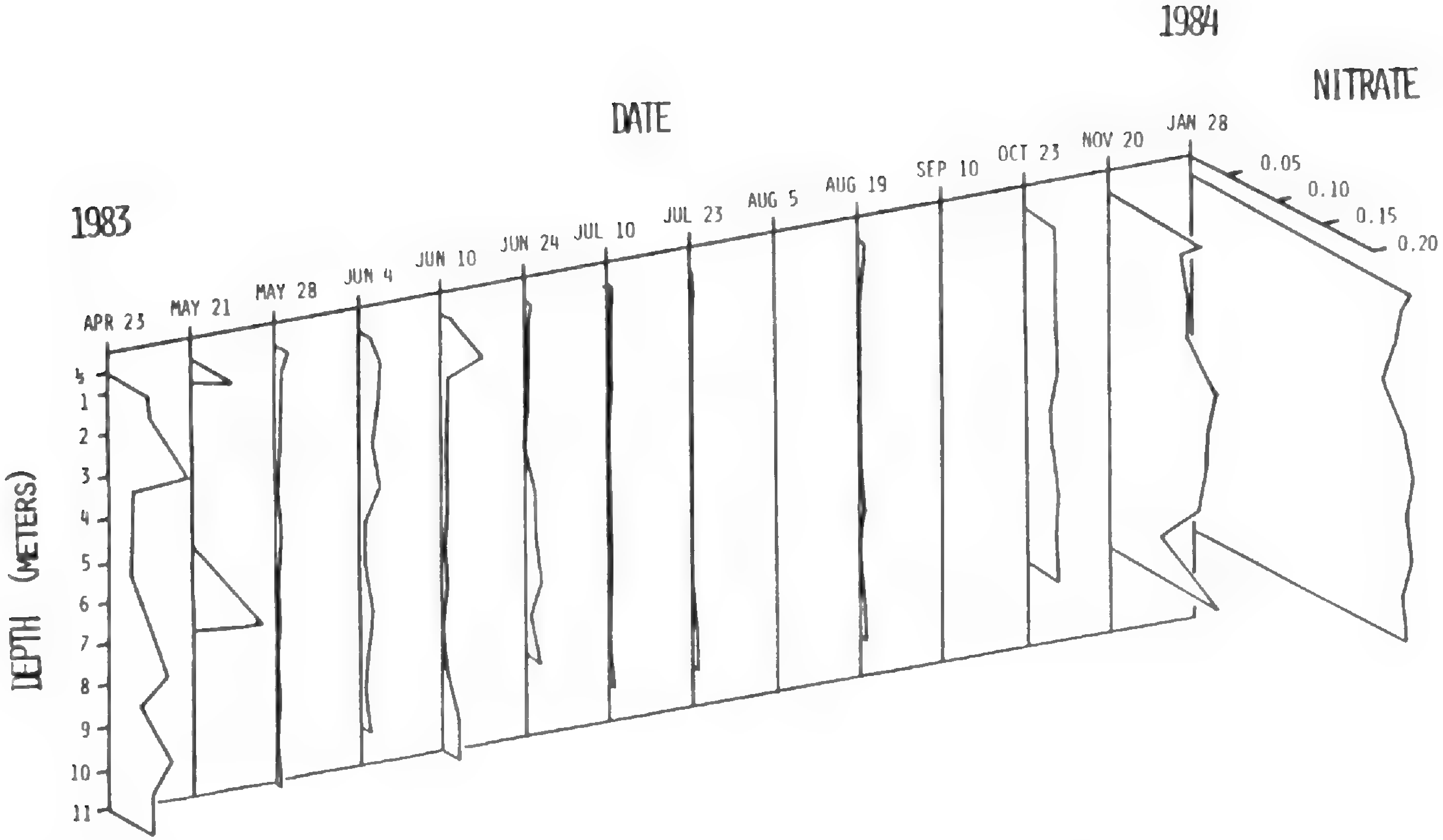

Figure 2. Nitrate concentrations versus depth and time in Danbury Bay (Site 1), Candlewood Lake, CT.

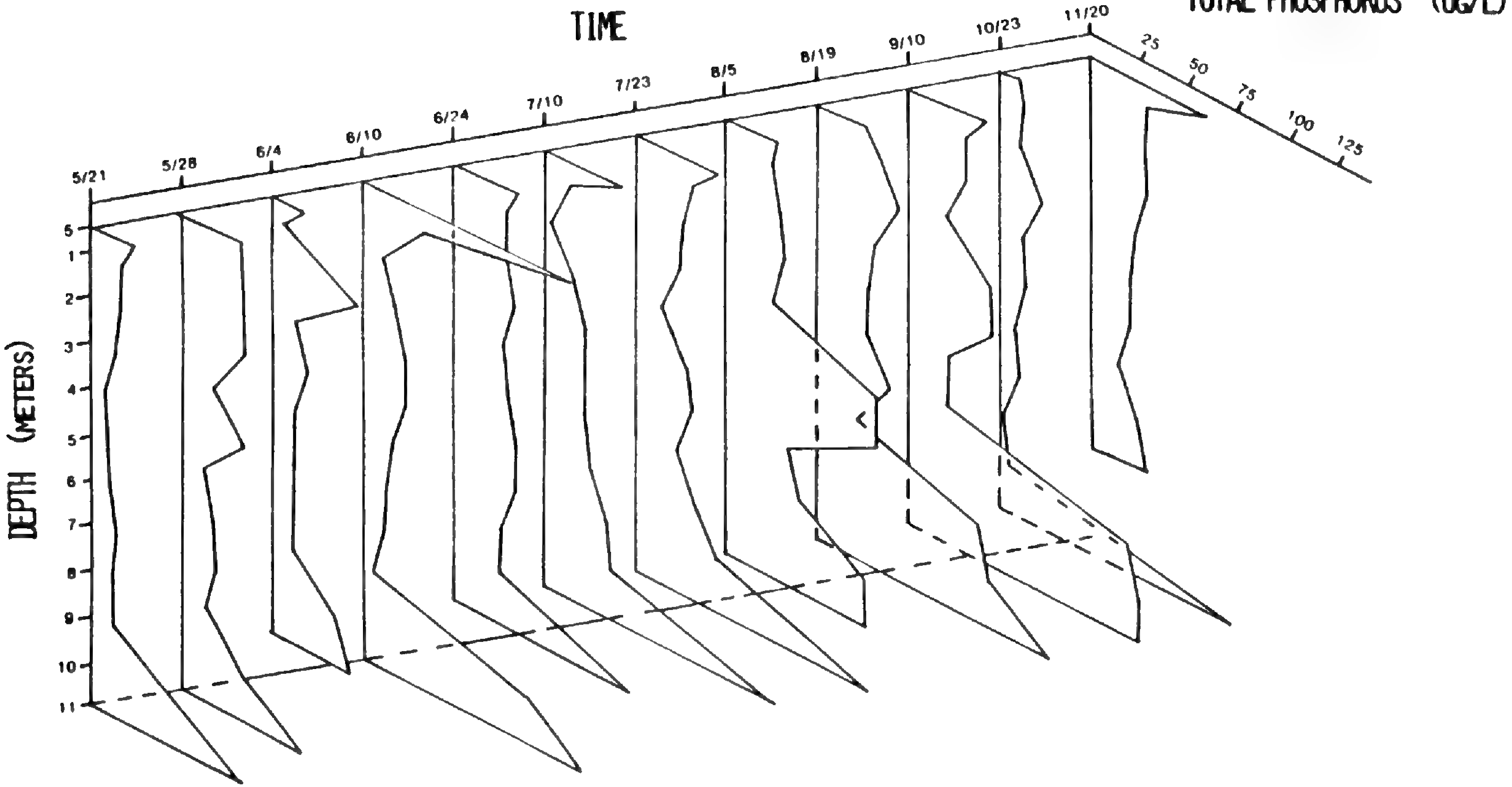

Figure 3. Total phosphorus versus depth and time in Danbury Bay (Site 1), Candlewood Lake, CT.

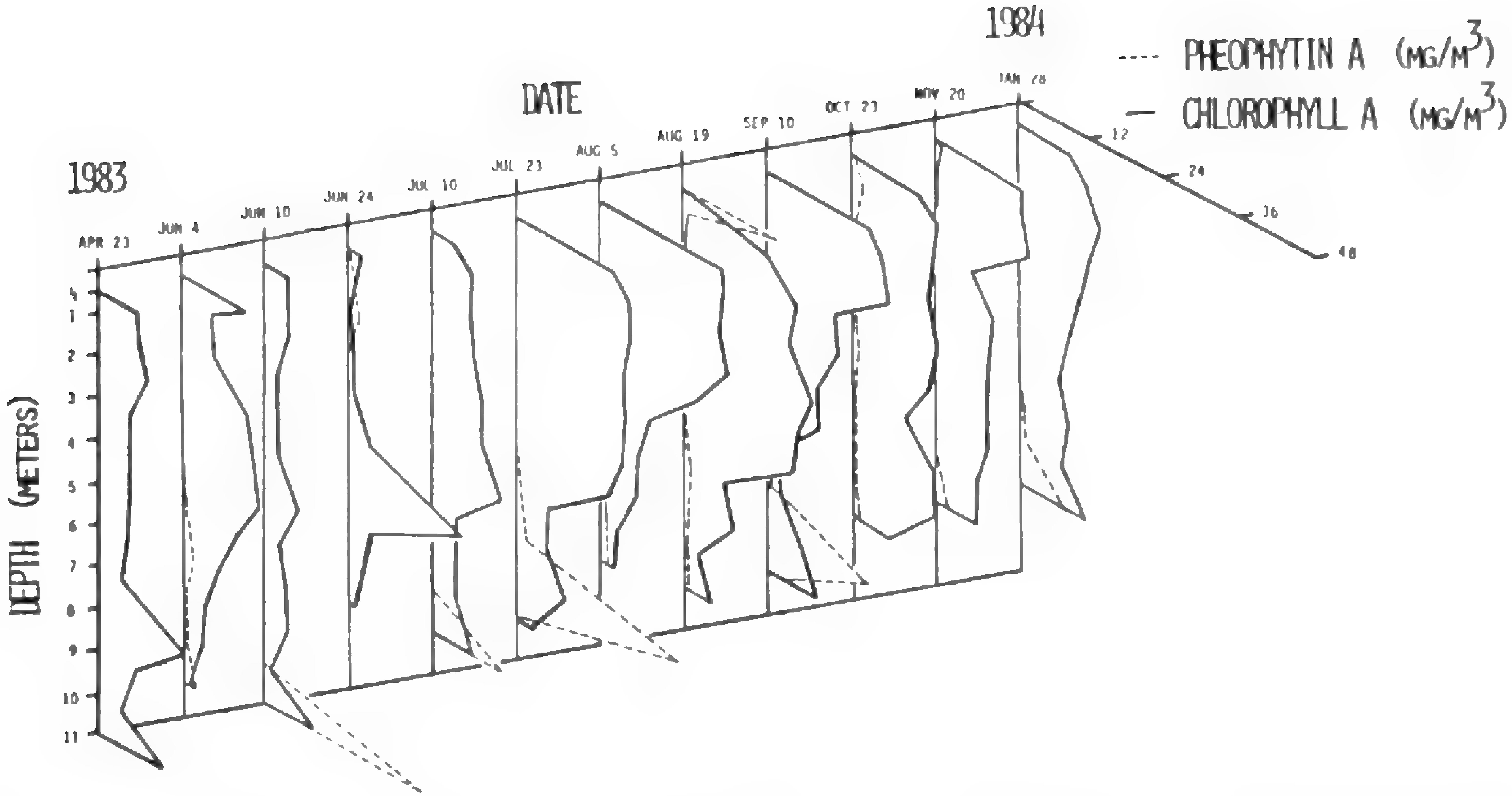

Figure 4. Chlorophyll a and phaeophytin a concentrations versus depth and time in Danbury Bay (Site 1), Candlewood Lake, CT. Concentrations estimated by the Lorenzen Method. ____ chlorophyll a _ _ _ phaeophytin a

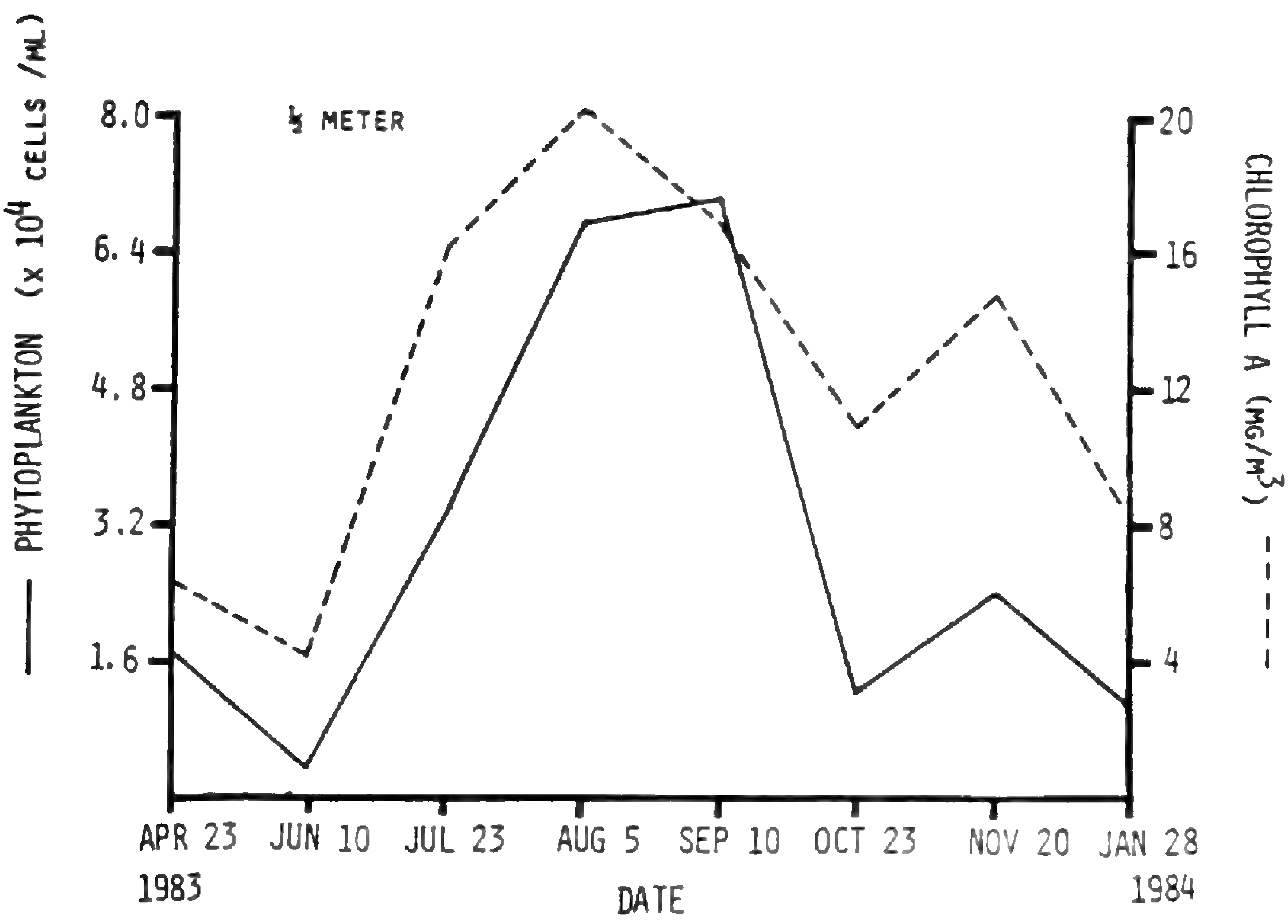

Figure 5. Seasonal levels of phytoplankton and chlorophyll a at 0.5 in Danbury Bay (Site 1), Candlewood Lake, CT. —— phytoplankton a – – – chlorophyll a

the Cyanophyceae dominated the lake's phytoplankton community, accounting for 89% of all cells. Concentrations of phytoplankton in surface waters ranged between 10^4 and 10^5 cells/ml, which was comparable to previous studies. However, we found that moderately high surface phytoplankton concentrations were present throughout the epilimnion (6–8 m) from June to September. Thus, following a calm period, the epilimnetic blue-green population could migrate to the surface after the formation of pseudovacuoles, to form an extensive bloom. Such bloom formation was observed during the study in several bays following calm periods. However, because of its long fetch, surface waters in the lake are generally well mixed, preventing surface migrations of the blue-greens.

In 1980 and 1981, the Connecticut Department of Environmental Protection reported mean ratios of total nitrogen to phosphorus greater than 15:1 and concluded that phosphorus was the limiting nutrient (DEP, 1983). The higher phosphorus concentrations recorded in 1983 could have led to periods of nitrogen deficiency. If so, a shift toward nitrogen-fixing taxa might be expected. In summer 1981, the phytoplankton were at least 61% Oscillatoriaceae, non-nitrogen-fixing blue-green algae (DEP, 1983), but in 1983, 67% of the algae were Nostocaceae, a blue-green family characterized by heterocystic taxa and presumably nitrogen-fixing. Thus, while the lake remained primarily a blue-green-dominated lake, a shift toward nitrogen-fixing taxa was evident, which enabled the blue-green algae present in 1983 to compensate for nitrogen-poor conditions. This finding could be an indication that nitrogen rather than phosphorus was, at times, the limiting nutrient in the lake.

Death and decomposition of macrophytes result in the release of nutrients, especially phosphorus, into the water column (Nichols and Keeney, 1973; Strange, 1976). Based on tissue phosphorus levels and the determination of macrophyte population numbers, it was estimated that the phosphorus concentrations in Danbury Bay could double if all tissue phosphorus were released (Simpkins, Cassia, and Siver, 1984). If the macrophytes were killed with the chemical herbicide 2,4-D as has been proposed, phosphorus could be released in large amounts. This death, in turn, could lead to an immediate increase in Nostocacean algae, especially *Anabaena flos-aquae* and *Aphanizomenon flos-aquae*.

Aquatic vascular plants may obtain their phosphorus in two ways, either by removing it from the sediments via root systems, or by absorbing it from the water column through the leaves (Wetzel, 1983). The effect that control of these macrophytes would have on the phytoplankton would depend on which system the macrophytes are using to obtain phosphorus. If they are acting as pumps, removing phosphorus from the sediments, their removal would negate a source of phosphorus to the phytoplankton and phytoplankton concentrations might decrease. Conversely, if the weeds are absorbing phosphorus from the water column, they represent competition for phosphorus to the algae. Thus, their control would remove competitive pressure from the algae and phytoplankton concentrations might increase.

Chlorophyll a concentrations have often been used as estimates of productivity and biomass (Kalff and Knoechel, 1978; Wetzel, 1983) as well as a parameter to indicate lake trophic status (Vollenweider, 1979; Wetzel, 1983). The range of chlorophyll a found in the present study (0–44 mg/m^3) is most closely associated with a eutrophic lake (Vollenweider, 1979). The correlation between phytoplankton and chlorophyll a concentrations indicated a seasonal succession pattern with a major summer peak (Figure 5). Thus, chlorophyll data could be used to estimate the phytoplankton concentrations in Candlewood Lake which were not enumerated in the present study. Based on these data, large seasonal algal maxima were observed at all six sites in the lake during the summer, with concentrations between 10^4 and 10^5 cells/ml. These concentrations were similar to those found by the Connecticut DEP in 1979–1981 (DEP, 1983). Since winter concentrations were also similar, it appears that the seasonality of phytoplankton cell concentrations has remained the same over the last 5 years, suggesting eutrophication of the lake (Wetzel, 1983).

The similar phytoplankton concentrations found at all six sites (Table 1) was unexpected since the sites were spread over 6 miles, and because of the highly dissected morphological nature of the lake. The horizontal distributions of phytoplankton may, in fact, be similar throughout the lake.

Based on data from this study, Candlewood Lake is a eutrophic lake. Because the change in trophic status of the lake occurred over a relatively short period of time (10 years), it is probable that reversion to an early mesotrophic condition could also occur rapidly if the nutrient load into the lake were reduced, much as it was in Lake Washington (Edmundson, 1970).

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DEPARTMENT OF BIOLOGICAL
AND ENVIRONMENTAL SCIENCES
WESTERN CONNECTICUT STATE UNIVERSITY
DANBURY, CONNECTICUT 06810

NEW WOOL-ALIEN CRUCIFERAE (BRASSICACEAE) IN EASTERN NORTH AMERICA: *LEPIDIUM* AND *SISYMBRIUM*

Ihsan A. Al-Shehbaz

ABSTRACT

The African *Sisymbrium turczaninowii, Lepidium africanum,* and *L. schinzii* and the South American *L. bonariense* are reported for the first time for North America. The Eurasian *S. loeselii* and the North American *L. austrinum, L. lasiocarpum,* and *L. oblongum* are new to the southeastern United States. All eight species were collected from waste grounds around wool-combing mills in South Carolina. A key to the eastern North American species of *Lepidium* is given.

Key Words: Cruciferae, Brassicaceae, *Lepidium, Sisymbrium,* wool-alien weeds, North America, South Carolina

INTRODUCTION

Many noxious weeds became naturalized in eastern North America shortly after their initial introductions in the seventeenth century by early European settlers. Ballast, wool, imported seed stocks, and agricultural products were important carriers of small fruits and seeds of numerous exotic plants. Fruits with hooks or spines are easily dispersed by clinging to animal wool or fur. Although a very few genera of the Cruciferae possess such fruits, the majority have relatively small seeds often capable of exuding mucilage when moistened. Such seeds can effectively be transported by adhering to uncleaned fleeces. It is not surprising, therefore, that many alien crucifers are common inhabitants of waste grounds around wool-combing mills.

This study is based on specimens collected in South Carolina by Harry E. Ahles and John G. Haesloop from waste grounds around the Santee Wool-Combing Mill (near Jamestown on route 45, Berkeley County) and around the Wellman Wool-Combing Mill (north of Johnsonville on route 41, Florence County). All specimens cited are deposited in NCU. This paper deals with eight species, of which three of *Lepidium* and one of *Sisymbrium* have not been previously recorded for North America.

LEPIDIUM

Species of *Lepidium* are probably the most common and successful crucifers of wool-alien flora. Their success may be attributed to their small mucilaginous seeds, their abundance on all continents but Antarctica, their weedy tendencies, and most importantly their predominantly autogamous breeding system. Seed characters and abundance of the species are important for adherence of seeds to the wool, while the breeding system and weediness are essential for the establishment of plants in their new habitats. As described below, some of the species have been collected from the same locality for three or four consecutive years, but the present fate of most of them is unknown.

Despite significant morphological differences between *Lepidium virginicum* L. and *L. densiflorum* Schrader, a few authors (e.g. Radford et al., 1968; Smith, 1978) have not recognized the latter or have reduced it to a synonym of the former. *Lepidium virginicum* usually has conspicuous petals and accumbent cotyledons; the petals, however, may abort in flowers which develop toward the end of the season, and the cotyledons are incumbent in some of its western North American varieties. In *L. densiflorum* the petals are either absent or aborted and the cotyledons are always incumbent. It is possible, therefore, to confuse the two species. *Lepidium densiflorum* tends to have fruits smaller than those of *L. virginicum,* but fruit size is unreliable for distinguishing the western North American plants of both species. The type of pubescence on the infructescence axis and, to a lesser degree, the shape of the fruit (*see* couplet N of the key below) are very useful in separating them.

The following key is provided to aid the identification of 14 native and exotic eastern North American lepidiums, including three recorded here as new for the continent. The European *L. latifolium* L. and *L. heterophyllum* (DC.) Bentham are sporadically distributed in New England, New York, and New Jersey, but neither has been reported from the Southeast. The native *L. austrinum* Small, *L. lasiocarpum* Nutt., and *L. oblongum* Small are very rare in the eastern limits of their natural ranges in Arkansas and Louisiana, but are widespread in California, the southwestern states, and northern and central Mexico. Undoubtedly, these last three have been introduced into South Carolina on imported wool, and are recorded here as well. Each of the six numbered species is further described following the key.

Key to the eastern North American species of *Lepidium*

A. Upper cauline leaves perfoliate or sagittate.
  B. Upper leaves perfoliate, ovate to orbicular; basal leaves bipinnatisect; fruiting pedicels glabrous; flowers yellow; seeds winged .... *L. perfoliatum* L.
  B. Upper leaves sagittate, oblong to linear or lanceolate; basal leaves undivided to rarely lobed; fruiting pedicels densely pubescent; flowers white; seeds wingless.
    C. Annuals or biennials; stems usually solitary at the base; fruits densely covered with vesicles; style included or slightly exserted from the apical notch of fruit; anthers yellow .... *L. campestre* (L.) R. Br.
    C. Perennials; stems several from the base; fruits without or with a few vesicles; style usually exserted 1 mm or more beyond the apical notch of fruit; anthers purple .... *L. heterophyllum* (DC.) Bentham
A. Upper cauline leaves tapering to the petiole or the base.
  D. Fruits 5–6 mm long; stamens 6; cotyledons 3-lobed .... *L. sativum* L.
  D. Fruits 1.5–3.5 (–4) mm long; stamens 2 (6 in *L. latifolium*); cotyledons entire.
    E. Fruiting pedicels erect-appressed; nectar glands filiform, 0.3–0.6 mm long; stems with retrorse, flattened, scalelike trichomes .... **6.** *L. schinzii* Thell.
    E. Fruiting pedicels ascending to spreading; nectar glands triangular or round, less than 0.2 mm long; stems glabrous or pubescent, without scalelike trichomes.
      F. Stoloniferous perennials, (50–) 70–130 cm high; fruits wingless and not notched at apex; stamens 6; stigma 2–3 times broader than the style; petals longer than the sepals .... *L. latifolium* L.
      F. Annuals or biennials, 10–45 cm high, rarely perennials to 75 cm high (*L. africanum*); fruits winged and notched at apex; stamens 2; stigma about as wide as the style; petals much shorter than the sepals (longer in *L. virginicum*).

G. Fruits pubescent or only ciliate at margin.
  H. Fruits with subappressed trichomes, lower surfaces of fruiting pedicels glabrous .... **2.** *L. austrinum* Small
  H. Fruits with spreading trichomes, lower surfaces of fruiting pedicels pubescent .... **4.** *L. lasiocarpum* Nutt.
G. Fruits glabrous.
  I. Petals conspicuous, equalling to twice as long as the sepals .... *L. virginicum* L.
  I. Petals inconspicuous, rudimentary, or absent, always shorter than the sepals.
    J. Upper cauline leaves pinnatifid to laciniate; axis of the infructescence with trichomes to 0.8 mm long.
      K. Fruiting pedicels 1.5–2 (–2.5) mm long, stems usually prostrate .... **5.** *L. oblongum* Small
      K. Fruiting pedicels (2–) 3–4.5 mm long, stems usually erect or ascending .... **3.** *L. bonariense* L.
    J. Upper cauline leaves entire, serrate, or dentate; axis of the infructescence glabrous, minutely papillose, or with trichomes usually less than 0.1 mm long.
      L. Basal leaves bi- or tripinnatisect, seeds wingless, lower surfaces of young fruiting pedicels sparsely papillose, apical wing of fruit subacute, plants fetid .... *L. ruderale* L.
      L. Basal leaves once pinnatifid to undivided, seeds narrowly winged or margined (wingless in *L. africanum*), lower surfaces of young fruiting pedicels glabrous, apical wing of fruit obtuse, plants not fetid.
        M. Fruits oblong or rarely oblong-ovate, seeds wingless.... **1.** *L. africanum* (Burm. *f.*) DC.
        M. Fruits orbicular to broadly ovate or obovate, seeds with a marginal or distal narrow wing.
          N. Axis of the infructescence with straight, usually subclavate, minute papillae; fruits

obovate to oblong-obovate or rarely suborbicular, usually widest above the middle; cotyledons always incumbent .... *L. densiflorum* Schrader

N. Axis of the infructescence with curved, usually subappressed, minute trichomes, rarely glabrous; fruits orbicular to broadly ovate, widest at or below the middle, cotyledons accumbent or obliquely so, very rarely incumbent .. *L. virginicum* L.

1. **Lepidium africanum** (Burm. *f*) DC.

Specimens examined: South Carolina. Jamestown, *Ahles & Haesloop 22599; Ahles & Haesloop 25814; Ahles & Haesloop 40523;* Johnsonville, *Ahles & Haesloop 53524.*

This species is a native of tropical and southern Africa. It is naturalized in Australia and is a wool-alien in Britain (Hewson, 1982; Ryves, 1977). It is reported here from North America for the first time. *Lepidium africanum* closely resembles *L. ruderale* but differs from it in its larger size, undivided basal leaves, and arcuate fruiting pedicels. *Lepidium ruderale* has bi- or tripinnatisect basal leaves and straight fruiting pedicels. The origin of the material cited here is very likely Africa because of the presence of other African wool-alien species in the same localities.

2. **Lepidium austrinum** Small

Specimens examined: South Carolina. Jamestown, *Ahles & Haesloop 52818; Ahles & Haesloop 53361.*

This North American species is distributed in Texas, New Mexico, Oklahoma, Kansas, and northern and central Mexico. It has not been recorded from the southeastern United States. Hitchcock (1936) recognized *Lepidium austrinum* as a distinct species, but later (Hitchcock, 1945a) reduced it to *L. lasiocarpum* Nutt. var. *orbiculare* (Thell.) C. L. Hitchc. In my opinion, *L. austrinum* is sufficiently distinct to merit specific rank.

3. **Lepidium bonariense** L.

Specimen examined: South Carolina. Jamestown, *Ahles & Haesloop 40522.*

It was not possible to trace the origin of the seed material from which the above collection was derived. *Lepidium bonariense,* recorded here for the first time for North America, is indigenous to South America and is a widely naturalized weed in Australia, western Europe, and tropical and southern Africa (Hewson, 1982; Carvalho e Vasconcellos, 1964; Jonsell, 1975; Marais, 1970). I follow Hitchcock (1945b) and Thellung (1906) in treating this polymorphic species without infraspecific taxa. Thellung (1912, 1914) recognized eight varieties in *L. bonariense,* but I am unable to find adequate morphological grounds for maintaining most of them.

4. **Lepidium lasiocarpum** Nutt.

Specimens examined: South Carolina. Jamestown, *Ahles & Haesloop 22598; Ahles & Haesloop 38301.*

The native range of this species extends from Colorado westward into California and southward into the southwestern United States and adjacent northern Mexico. *Lepidium lasiocarpum* has been reported from Louisiana by Thomas & Allen (1982), but it is apparently a rare plant in that state. Of the eight varieties recognized by Hitchcock (1936, 1945a) in *Lepidium lasiocarpum,* the collections cited here belong to the type variety.

5. **Lepidium oblongum** Small

Specimens examined: South Carolina. Jamestown, *Ahles & Haesloop 22559; Ahles & Haesloop 38302; Ahles & Haesloop 53476.*

Lepidium oblongum is distributed from California eastward through the southwestern states, Kansas, and central Arkansas and southward into northern and central Mexico and Guatemala. Hitchcock (1945a) recognized two varieties in *L. oblongum.* All of the three collections cited here belong to the type variety.

6. **Lepidium schinzii** Thell.

Specimens examined: South Carolina. Johnsonville, *Ahles 40451* (2).

This is the first record of this South African species in the New World, and the collection cited must have been derived from seeds introduced from its native range. *Lepidium schinzii* is also a woolalien in Europe. It is easily distinguished from the other lepidiums in

North America by its appressed-erect fruiting pedicels and by its stems with retrorse, flattened, scalelike trichomes.

SISYMBRIUM

The genus *Sisymbrium* is represented in North America by an indigenous species, *S. auriculatum* A. Gray (Texas, New Mexico, and northern Mexico), and by six Eurasian weeds (Rollins, 1981). Almost all of the North American species assigned previously to *Sisymbrium* by Payson (1922) are now believed to belong to *Thelypodiopsis* Rydb. and *Schoenocrambe* Greene (Rollins, 1982). The following discussion deals with two species, of which one is a new addition to the New World's weed flora.

1. **Sisymbrium turczaninowii** Sond.

Specimens examined: South Carolina. Jamestown, *Ahles & Haesloop 42907;* Johnsonville, *Ahles 40434* (2).

This South African species has not been previously recorded from the New World. It is a densely pubescent perennial in its native habitat, but the specimens above are annuals with a sparse indumentum. The characteristic features of *Sisymbrium turczaninowii* are: pinnatifid, sessile upper cauline leaves with dentate lobes; ebracteate inflorescences; stout, short (1–2.3 cm), terete, erect siliques with antrorsely strigose valves; and small 0.7–0.8 × 0.3–0.5 mm), biseriate seeds.

2. **Sisymbrium loeselii** L.

Specimens examined: South Carolina. Jamestown, *Ahles & Haesloop 53808*; Johnsonville, *Ahles 53754.*

This Eurasian weed is abundant in the Canadian prairie provinces and in some of the mountain states (Rollins, 1981). It is sporadic in widely separated localities in New England, Pennsylvania, Michigan, and North Dakota, but has not been recorded from the southeastern states. *Sisymbrium loeselii* is eaily distinguished from the other sisymbriums in North America by the combination of its divaricate fruiting pedicels narrower than the siliques, the terete, short 1–4.5 cm) siliques not overtopping the floral buds, and its 4–7 mm long petals.

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ARNOLD ARBORETUM
HARVARD UNIVERSITY
22 DIVINITY AVE.
CAMBRIDGE, MA 02138

CURRENT STATUS OF *MAGNOLIA VIRGINIANA* IN MASSACHUSETTS

RICHARD B. PRIMACK, EDWARD HENDRY AND PETER DEL TREDICI

ABSTRACT

The sweet bay magnolia (*Magnolia virginiana* L.) from Gloucester, Massachusetts, was almost eliminated by flower collectors in the early 20th century from its one locality in New England. The population appears to have recovered since that time and now consists of approximately 129 multi-stemmed plants which have a total of 1800 stems. Approximately 33% of the plants produced fruits in 1984. Plants have shown a positive growth in height and number of stems in the two-year period, 1982–1984. No naturally occurring seedlings were evident. The population appears to be persisting through the vegetative vigor of existing plants, some of which may be long-lived. Seedlings grown from seed collected in the Gloucester stand in 1980 and transplanted back into the area in 1982 showed excellent survival (48%) and moderate growth as of 1984.

Key Words: *Magnolia*, rare plants, ecology, Massachusetts

INTRODUCTION

The sweet bay magnolia (*Magnolia virginiana* L.) has only one known population in New England, with the next population occurring 150 miles to the south on the eastern shore of Long Island (Little, 1971). The New England population of this small, freely-sprouting tree occurs in a swamp near the coast in Gloucester, Massachusetts. Since its discovery, this plant population has received the attention of both botanists and the general public because of status as a "southern" species growing far from its normal range. The residents of the Kettle Cove section of Gloucester, where the magnolia grows, were so enthusiastic over the discovery of the plant that they changed the name of the community to Magnolia in the 19th century. Del Tredici (1981) has reviewed in detail the history of the population, horticultural varieties of the species, and seed germination behavior. The purpose of this article is to present a statistical summary of the current status of the population, particularly in relation to the past condition of the population. These data will be used to determine whether current management of the site is appropriate.

HISTORICAL BACKGROUND

1623. The town of Gloucester was founded.

1806. Theophilus Parsons discovered the magnolia population while riding in a carriage along woodland road between Kettle Cove and Fresh Water Cove in Gloucester. The location described by Parsons (from Kennedy, 1916) is the "swamp on the western side of the road as you go from Manchester to Gloucester, and before you come to a large hill over which the road formerly passed. It grows so near the road as to be visible even to the careless eye of the traveler."

1814. Jacob Bigelow (1814) in the Plants of Boston stated that the magnolia "attains a height of a dozen feet, but is sometimes killed down to the roots by severe winters. . . . It grows plentifully in a sheltered swamp at Gloucester, Cape Ann."

1858. Henry David Thoreau (1962) visited the swamp on September 22. He described the magnolia bushes as being 2 to 7 feet in height. The susceptibility to frost-damage was again noted: "I saw last year's shoots, which had died down several feet, and probably will be the fate of most which has grown this year."

1875. People had begun collecting flowers from the magnolia plants to sell in Boston and Salem. So widespread had this practice become that George B. Emerson (1875) writing in A Report on the Trees and Shrubs Growing Naturally in the Forests of Massachusetts said that scores of trees had been broken down by people collecting flowers to sell.

1889. J. G. Jack (1889) confirmed how desperate the situation had become for this population: "So eagerly have the flowers been sought for by collectors and especially by those who wished to make money out of the sale of both plants and flowers, that there has been some apprehension that the day would soon come when the Magnolia could only be classed in New England floras as one of the indigenous plants of the past." In that same year, some hope for the protection of the population developed. Mr. Samuel E. Sawyer, the owner of the swamp, set aside the land to be managed as "Ravenswood Park", for the enjoyment of the public.

1913. Unfortunately, the condition of the population continued to deteriorate. C. E. Faxon (quoted in Kennedy, 1916) stated, "When I first visited the swamp some 45 years ago (roughly 1868) there were plenty of good specimens all about, sometimes 15 feet tall or more." However, by 1913, "only two little plants a few feet high had escaped the Magnolia hunters—such had been the destruction!"

1970. The trustees of Ravenswood Park recognized that the magnolias were being shaded out by the growth of large canopy trees of hemlock, white pine, and red maple. Consequently, a program of thinning out the large trees was initiated.

1980. Peter Del Tredici (1981) of the Arnold Arboretum observed that the magnolias appeared to be growing well and fruiting. He estimated that there were 40 to 50 multi-stemmed magnolia clumps, most being 6 to 12 feet in height, with one plant 18 feet in height. Del Tredici commented that the swamp at present must be more shaded than the past, as shown by the abundance of the shade-tolerant inkberry (*Ilex glabra*) which was not mentioned as being present by Jack (1889). Also, Jack (1889) listed the light-demanding cranberry (*Vaccinium macrocarpon*) as growing densely in the swamp, but this plant no longer grows there.

These scattered observations provide a picture of a magnolia population that was probably extensive in the early 19th century, declined greatly in the late 19th and early 20th century as a result of stems being broken down during collection of flowers, and then recovered to its present status. However, the exact status of the population is difficult to determine without a quantitative survey of the population in which individuals are tagged, mapped and measured through time.

MATERIALS AND METHODS

A study was initiated on November 14, 1982 by two of the authors (RBP and PDT), accompanied by two Boston University students. During this survey, every multi-stemmed plant clump was tagged with a metal tag, typically at shoulder height. For a few plants, there was some difficulty estimating what constituted one genetic or physiological individual, since stems are sometimes bent to the ground and root, forming new clumps of shoots at distances of up to 3 m from the original clump. After tagging, a rough map was made of the population and plants were evaluated for the following three characters:

1. HEIGHT was visually estimated to the nearest 0.3 m for the tallest stem in a clump. Estimates were improved by practicing on several plants measured with a tape-measure. Some error is probably associated with this estimate.
2. NUMBER OF STEMS for the plant was counted, with every shoot emerging from the ground counted as a separate stem. Often many new stems would develop from an existing stem which had been bent down and partially covered with leaves.
3. NUMBER OF FRUITS present on the plant. This number is a significant underestimate of fruit production since many fruits had already fallen off the plants.

The site was revisited on November 3, 1984, the field party consisting of the three authors and eleven Boston University students. Previously tagged plants were located, and measurements taken again on the three plant characters. The larger field party made it possible to survey the area more intensively and locate plants missed in the previous survey. This effort provided a confirmation of Wu's law of plant population biology, "The more you look, the more you see."

RESULTS

1982. 119 clumps were located and tagged, many more than had been anticipated. Heights of the clumps varied from 0.3 m to 8.4 m, with a mean of 3.6 m. Number of stems per clump varied from 1 to 64, with a mean of 15.2 stems. Many of these stems were relatively small and often less than 0.6 m in height. The total number of stems in the population is about 1800. Using Spearman Rank Correlations, there is no correlation between plant height and the number of stems ($r = 0.139$), indicating that these two measures of plant size are essentially independent of each other. The distribution of height in the population appears to be normal (Figure 1), indicative of a mature population in which adult trees are persisting and growing, but with relatively little regeneration by seed. The same pattern holds when number of stems per plant is examined (Figure 2): 32

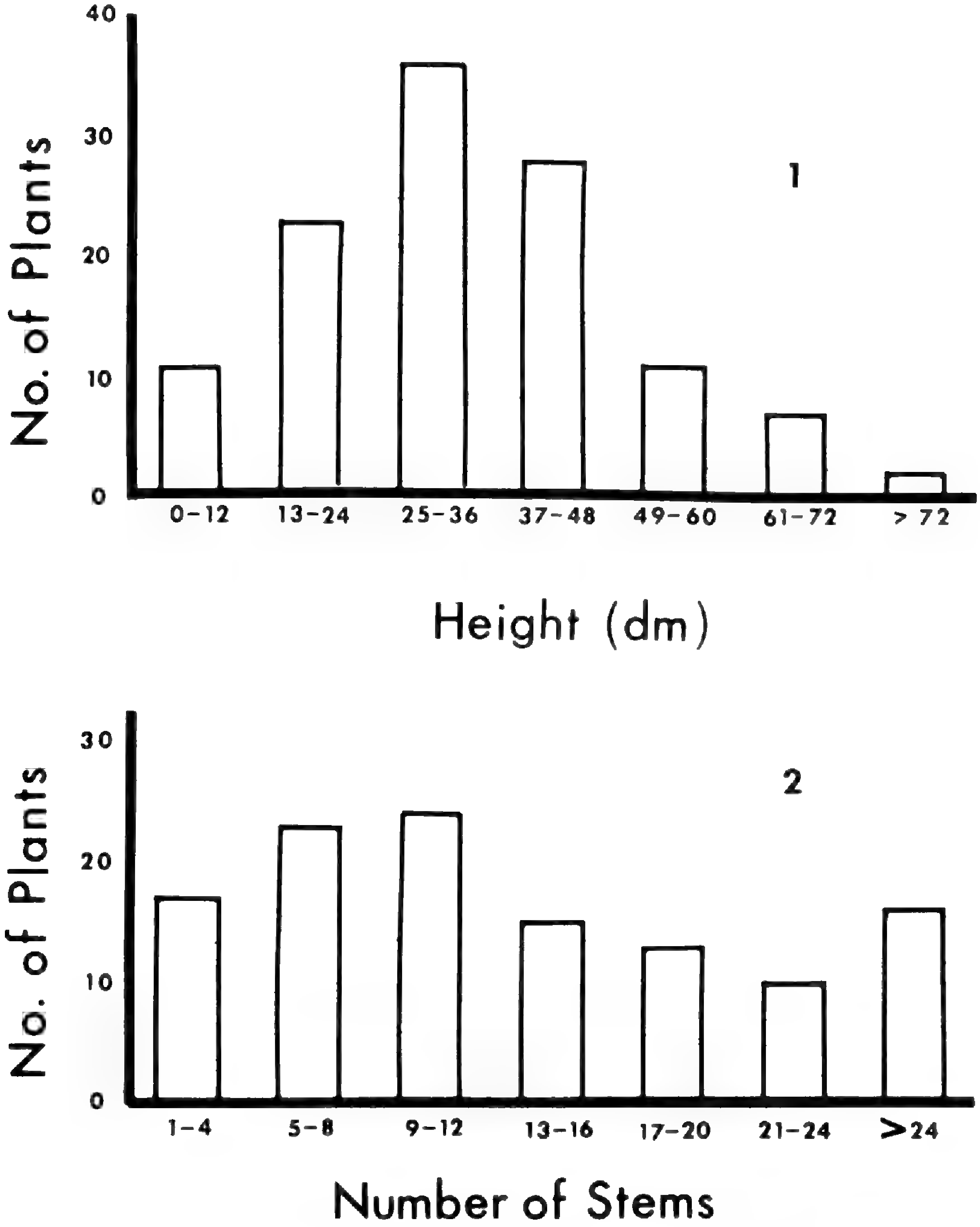

Figure 1-2. Distribution of plant height and number of stems per plant in the magnolia population in 1982. **1.** Plant height. **2.** Number of stems per plant.

plants had fruits, with an average of 6.7 fruits each; one plant had 37 fruits.

1984. Of the original 119 plants, 114 were re-located, 3 plants could not be found, and 2 plants were apparently dead; in addition, 15 new plants were located. While one of these plants may have been established from seed since 1982, the other 14 plants are clearly older plants that were overlooked in the 1982 census or were beyond the fringes of the area then surveyed. The larger size of the 1984 survey team made possible our locating these additional plants. 129 plants were tagged, mapped, and measured in 1984.

In 1984, mean plant height of the original plants was 3.9 m, a significantly greater height than in 1982, (t-test; $p < 0.05$). These results suggest that the population is increasing in height. Another indication of vegetative growth was that 72 out of 112 plants showed an increase in height, compared with 1982 measurements, while only 22 plants showed a decline in height; 18 plants measured no change.

Mean number of stems per plant of the original plants was 17.5, again a significant ($p < 0.05$) increase over 1982. The largest plant had 104 stems in 1984, while the same plant had only 64 stems in 1982. A total of 74 plants showed an increase in the number of stems over 1982, 24 plants showed a decrease, and 15 plants showed no change.

The fact that the new plants found in 1984 were probably just overlooked in 1982 is emphasized by the fact that they had a mean height (3.4 m) and a mean number of stems (12.8) which were smaller but reasonably similar to the values of the tagged plants.

A total of 42 plants produced fruit in 1984, representing 33% of the population. Of these same plants, 24 had also produced fruit in 1982, indicating some stability in the reproductive structure of the population. Fruiting plants produced an average of 5.1 fruits with a total of 214 fruits in the population. One plant produced 37 fruits.

In the fall of 1980, seeds were collected from the site and grown in pots at the Arnold Arboretum. In May 1982, 500 of these 18 month-old seedlings were transplanted back into the swamp at two locations, one about 50 meters from the northern edge of the wild population and the other at the southern edge. Prior to planting, the canopy was opened up in these two areas by removal of several large trees. As of November 1984, 239 of the seedlings (48%) were still alive. The tallest plants were about 75 cm high with most plants in the 15–25 cm range. When planted, the seedlings were all under 10 cm. While this increase in height is not particularly dramatic, it is not much less than that shown by ten seedlings from the same seed lot grown under light shade in the outdoor nursery at the Arnold Arboretum in Jamaica Plain, Mass. As of February, 1985, these nursery seedlings planted at the same time as the Ravenswood plants, ranged in height from 20 to 54 cm, with an average height of 31 cm.

DISCUSSION

The population of sweet bay magnolias in Gloucester has clearly recovered from those dismal days of the late 19th and early 20th century when all of the stems were broken down. The population is healthy in many ways. Roughly 35% of the plants have been flowering and fruiting, suggesting that the plants are in good physiological condition. There is an abundance of plants (129 clumps), a great increase over the 2 plants observed in 1913. The number of stems observed in 1982 (approximately 1800) is impressive, and argues for the health of the population, even though many of the stems are small. Measurements of height and number of stems from 1982 and 1984 indicate that the average size of individuals is increasing. Further, the human pressure on the population has obviously decreased; the area is now in a well-managed park and people no longer collect the flowers to sell and probably rarely visit the swamp where the magnolias grow. These factors all indicate that the population is in good condition.

The fact that no seedlings or young plants were noted in the Ravenswood population, despite good seed production, indicates that the population is under some limitation. Even with the tree thinning of 1970, the swamp is still too shaded to allow seedling establishment and consequently a self-maintaining magnolia population. The continued presence of shade-tolerant inkberry and the absence of light-demanding cranberries further emphasizes that the swamp is probably too shaded for magnolia establishment.

The main mechanism maintaining the population at present is clearly vegetative reproduction, involving abundant sprouting from the root systems and rooting of stems that have been bent down by large branches falling from the trees above. This rooting of prostrate stems provides a mechanism for limited lateral movement of a clone. It is a reasonable speculation that most of the magnolia plants present in the swamp today were there in the early 19th century when the population was first discovered, and have maintained themselves until the present time by sending up new stems from the persistent root system, much like the chestnut tree (*Castanea dentata*) does today. Magnolia plants in southern savannas sprout readily after fires, and these Gloucester magnolias are adapted to sprout following a severe frost which kills the stems. This ability to sprout pre-adapted the species for recovery when stems were broken during collection of flowers. Further, we speculate that several of the larger magnolia clumps might have been present in the swamp for several thousand years, or ever since the population was first established following retreat of the glacier. It is not possible to prove or disprove this speculation at present. However, detailed studies of isozymic variation on this population, as has been done for salt-marsh cordgrass (Silander, 1979) and alder (Huenneke, 1985), might reveal the extent to which individual genotypes have spread through the swamp as a result of vegetative reproduction.

An alternative hypothesis would be that *Magnolia virginiana* invaded the swamp via bird dispersal at some point in the eighteenth century following logging and/or burning of the swamp. Following this initial invasion, the magnolias did not become a prominent feature of the landscape until 1804, when first noticed by Theophilus Parsons. This hypothesis would explain why the plant went undiscovered for so long in an area that was settled in 1623.

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R. B. P. AND E. H.
BIOLOGY DEPARTMENT
BOSTON UNIVERSITY
BOSTON, MA 02215

P. D. T.
ARNOLD ARBORETUM OF
HARVARD UNIVERSITY
JAMAICA PLAIN, MA 02130

STUDIES IN THE *ARISTIDA* (GRAMINEAE) OF THE SOUTHEASTERN UNITED STATES. IV. KEY AND CONSPECTUS.[1]

KELLY W. ALLRED

ABSTRACT

The grass genus *Aristida* in the southeastern United States is reviewed. Twenty species are present in the region, all indigenous to the area. New combinations proposed are *Aristida purpurescens* Poir. var. *tenuispica* (Hitchc.) Allred and var. *virgata* (Trin.) Allred.

Key Words: *Aristida*, floristics, southeastern United States

This paper concludes a series of investigations of the *Aristida* of the southeastern United States. The first paper dealt with the *purpurescens-tenuispica-virgata* complex, the second with *A. intermedia* and *A. longespica*, and the third compared the *lanosa* and *palustris* entities (Allred, 1984a, 1985a, b). All were phenetic in nature and based solely on herbarium collections. These studies were preparatory to a treatment of this genus for the Vascular Flora of the Southeastern United States. Several questions have arisen and remain unanswered by the studies. For example, little is known about chromosome numbers, breeding systems, or extent of ecotypic variation of these grasses. It is hoped that such information can be acquired from future systematic studies of this troublesome but interesting genus.

Examination of *Aristida* collections from 26 herbaria (*see* Acknowledgments) resulted in the documentation of 20 species for the region covered by the Vascular Flora of the Southeastern United States project (Alabama, Arkansas, Delaware, Florida, Georgia, Kentucky, Louisiana, Maryland, Mississippi, North Carolina, South Carolina, Tennessee, Virginia, and West Virginia). For all taxa recognized herein, one of the types or a photo of the type was seen. Although all taxa were indigenous to the southeastern United States, there are three records of adventives worthy of note. Gleason and Cronquist (1963) reported *A. adscensionis* L. as being "rarely

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adventive" in the northeastern United States, and Hitchcock and Chase (1951) reported it as far east as Missouri, but no specimens were seen of this species from the southeast flora region. In addition, there were several collections of Australian species in Jamestown, South Carolina, from around a wool-combing mill. These grasses combined features of *Aristida armata* Henrard, *A. benthamii* Henrard, and *A. inaequiglumis* Domin; they are easily distinguished from any North American *Aristida* by a groove (sulcus) on the ventral side of the floret, formed by the involute margins of the lemma that do not completely enclose the palea and flower. Also, *Aristida divaricata* Willd. was collected from the Soil Conservation Service Nursery at Chapel Hill, North Carolina in 1941. This species is found on the dry southwestern plains and will probably not become naturalized as part of the southeastern flora.

A few terms should be defined. The *awn column* is formed by the connivent or coalescent bases of the awns above the lemma, and is usually twisted (for example, *Aristida tuberculosa*). This structure differs from the *beak* of the lemma, which is the slender, narrowed terminal portion of the lemma body just below the awns; it is also often twisted (for example, *A. spiciformis*). The *awns* themselves are free from one another, and are measured from the summit of the beak or awn column to the tip of the awn.

At this point in our understanding of these *Aristida*, it would be unwise to speculate on the phylogeny of the taxa, but it may be helpful to give some indication of the apparent morphologic relationships among them. The groupings that follow are based only on external morphology and the intuitive insights gained after examining several thousand herbarium specimens. The taxa included within a group may be considered to be generally similar to one another, but no biologic relationships are implied. The groups are informal, with no taxonomic standing or rank, and in some cases are based on similar such groups found in Hitchcock and Chase (1951).

Group *Dichotomae*. All of these taxa have a tendency toward coiling of the central awn; this coiling is most pronounced in *Aristida dichotoma* and *A. basiramea*, and only slightly developed in *A. longespica*. *Aristida oligantha* and *A. ramosissima* intergrade, as do *A. dichotoma* and *A. basiramea*.

A. oligantha
A. ramosissima
A. dichotoma vars. *dichotoma* and *curtissii*
A. basiramea
A. longespica vars. *longespica* and *geniculata*

Group *Tuberculosae.* These taxa are members of the generic section *Arthratherum,* in which the lemma is jointed at the summit and breaks from the awn column. Our species differ mainly in size of the spikelet parts.

A. tuberculosa
A. desmantha

Group *Purpureae.* This group enters our region only in a few scattered localities in Arkansas and Louisiana. The nearest relatives are all plains and desert taxa of the southwestern United States, Mexico, and South America.

A. purpurea vars. *purpurea* and *longiseta*

Group *Purpurescentes.* More heterogenous than the others, this group contains taxa that are very similar to *Aristida purpurescens* (*tenuispica, virgata, condensata, gyrans*) as well as taxa that seem to fit nowhere else but have a general similarity of panicle or spikelet. *Aristida stricta, A. rhizomophora,* and *A. lanosa* have peculiar vegetative features that distinguish them.

A. purpurescens vars. *purpurescens, tenuispica,* and *virgata*
A. condensata
A. gyrans
A. palustris
A. mohrii
A. simpliciflora
A. stricta
A. lanosa
A. rhizomophora

Group *Divaricatae.* Used by Hitchcock and Chase (1951) for species with abruptly spreading panicle branches, this group is expanded somewhat to include otherwise similar species with reduced lateral awns. *Aristida floridana* is tentatively placed here because of its similarity to *A. ternipes,* a species of the western deserts, which in turn is very close to *A. patula* and other members of the group *Divaricatae.*

A. patula
A. floridana

Group *Spiciformes.* This *Aristida* group shows a parallel development to the group *Tuberculosae* in the long, twisted lemma beak. It differs, however, in that the beak appears to be an elongation of the lemma body rather than a twisting together of the awns. Also, the dense panicle and unequal, awned glumes are distinctive in this group.

A. spiciformis

Following the key is a conspectus for each numbered species which gives the correct name and author, pertinent synonyms, identifying features, general habitat and distribution, and miscellaneous notes. The distribution data are provided only for those states covered by the "Southeastern Flora," and not the entire range of the species. A representative spikelet of each taxon is illustrated with figures taken from Henrard (1929, 1932).

KEY TO THE SPECIES

1. First glume 3–7 nerved .... (2)
  2. Central awn of lemma 0.9–3 cm long; awn of second glume 3–7 mm long .... **15.** *A. ramosissima*
  2. Central awn of lemma 3–7 cm long; awn of second glume 7.5–17 mm long .... **10.** *A. oligantha*
1. First glume 1–2 nerved .... (3)
  3. Central awn spirally coiled at the base like a corkscrew....(4)
    4. Lateral awns 4 mm or less long, erect .....**4.** *A. dichotoma*
    4. Lateral awns 5–12 mm long, spreading.... **1.** *A. basiramea*
  3. Central awn not spirally coiled, straight to curving or contorted, but not corkscrew-like .... (5)
    5. Lateral awns markedly reduced, 1/3 or less the length of the central awn .... (6)
      6. Plants annual; panicle narrow, rarely wider than 5 cm, the branches erect .... **8.** *A. longespica*
      6. Plants perennial; panicle open, almost always wider than

5 cm, the branches spreading .... (7)

7. Lateral awns 0–1 mm long; central awn sickle-shaped .... **5.** *A. floridana*

7. Lateral awns 3–10 mm long; central awn straight to somewhat flexuous but not sickle-shaped.......... .... **12.** *A. patula*

5. Lateral awns well developed, at least 1/2 the length of the central awn .... (8)

8. Leaf blades tightly involute, stiff and wiry, the young blades pilose on the lower (outer) surface near the midrib especially toward the base, also often densely pilose at the throat and collar region .... **19.** *A. stricta*

8. Leaf blades, flat, or if involute then glabrous at the throat and collar region .... (9)

9. Nodes of panicle axis with a tuft of lanose or floccose hairs; sheaths lanose or floccose, the hairs cobwebby, kinked and intertwined .... **7.** *A. lanosa*

9. Nodes of panicle axis glabrous or sparsely pilose; sheaths glabrous to pilose, the hairs straight, not cobwebby, and usually appressed .... (10)

10. Lemma body separated from the awns or awn column by a joint (zone of articulation), the body and awns eventually disarticulating (check mature spikelets) .... (11)

11. Panicle spiciform, dense, compact, the spikelets very congested, the branches appressed; plants perennial, the culms simple or sparingly branched .... **18.** *A. spiciformis*

11. Panicle open, loose, somewhat fan-shaped, the spikelets only slightly congested, the branches ascending to spreading; plants annual (may be robust), the culms usually much branched .... (12)

12. Glumes, at least the second, longer than 2 cm; awn column (formed by a twisting together of the awn bases) 8–15 mm long; callus mostly 3–4 mm long .... **20.** *A. tuberculosa*

12. Glumes both shorter than 2 cm; awn column 2–5, rarely 7, mm long; callus mostly 2–2.5 mm long . . . . **3.** *A. desmantha*

10. Lemma body passing directly into the awns, without a joint of articulation, the body and awns not disarticulating . . . . (13)

13. Summit of lemma with an obvious, elongated beak mostly 10–30 mm long (rarely only 7 mm long) . . . . **18.** *A. spiciformis*

13. Summit of lemma without a beak, or if slightly beaked then obscure and less than 7 mm long . . . . (14)

14. Panicle open at maturity, the branches widely spreading to reflexed from axillary pulvini; first glume longer than the second . . . . **12.** *A. patula*

14. Panicle narrow, with mostly erect-appressed or ascending branches without axillary pulvini, if the branches somewhat open and drooping (in *A. purpurea* and *A. rhizomophora*) then the first glume shorter than the second . . . . (15)

15. Plants with vigorous thick rhizomes; basal sheaths becoming markedly fibrous in age and shredding into thread-like segments . . . . **16.** *A. rhizomophora*

15. Plants tufted, lacking rhizomes; basal sheaths not becoming fibrous and not shredding into thread-like segments . . . . (16)

16. Spikelets borne singly at each node of the main axis, the inflorescence a spike or raceme . . . . **9.** *A. mohrii*

16. Spikelets at least two per node of the main axis, or borne on branches at least below, the inflorescence racemose or paniculate . . . . (17)

17. First glume 1/3 to 3/4 the length of the second glume . . . . (18)

18. Lemma awns 0.8–1.5 cm long; lemma 5–6 mm long . . . . **6.** *A. gyrans*

18. Lemma awns 2–10 cm long; lemma 6–16 mm long . . . . **13.** *A. purpurea*

17. First glume more than 3/4 the length of the second glume . . . . (19)

19. Plants annual . . . . **8.** *A. longespica*

19. Plants perennial . . . . (20)

20. Central awn 1.5–4 cm long; first glume prominently 2-keeled and 9–13 mm long in mature specimens .... **11.** *A. palustris*

20. Central awn 0.8–2.5 cm long; first glume mostly 1-keeled (2-keeled in some *A. purpurescens*) and/or 6–9 mm long .... (21)

21. Central awn about twice as thick as the lateral awns, divergent to arcuate-reflexed .... (22)

22. All three awns divergent to reflexed, somewhat contorted at the base; spikelets mostly two per node (occasionally 3), one pedicelled and one subsessile..... **17.** *A. simpliciflora*

22. Lateral awns (sometimes also the central) mostly erect to ascending, usually not contorted at the base; spikelets mostly many per node, but sometimes only two, pedicelled or subsessile .... **14.** *A. purpurescens*

21. Central awn about the same thickness as the laterals, erect to divergent .... (23)

23. First glume 1–4 mm longer than the second............... .... **14.** *A. purpurescens*

23. First glume no more than 1 mm longer than the second, or shorter .... (24)

24. Culms usually robust, the lower shoots 3–6 mm broad; panicle branches 4 cm or more long; first glume 1-nerved .... **2.** *A. condensata*

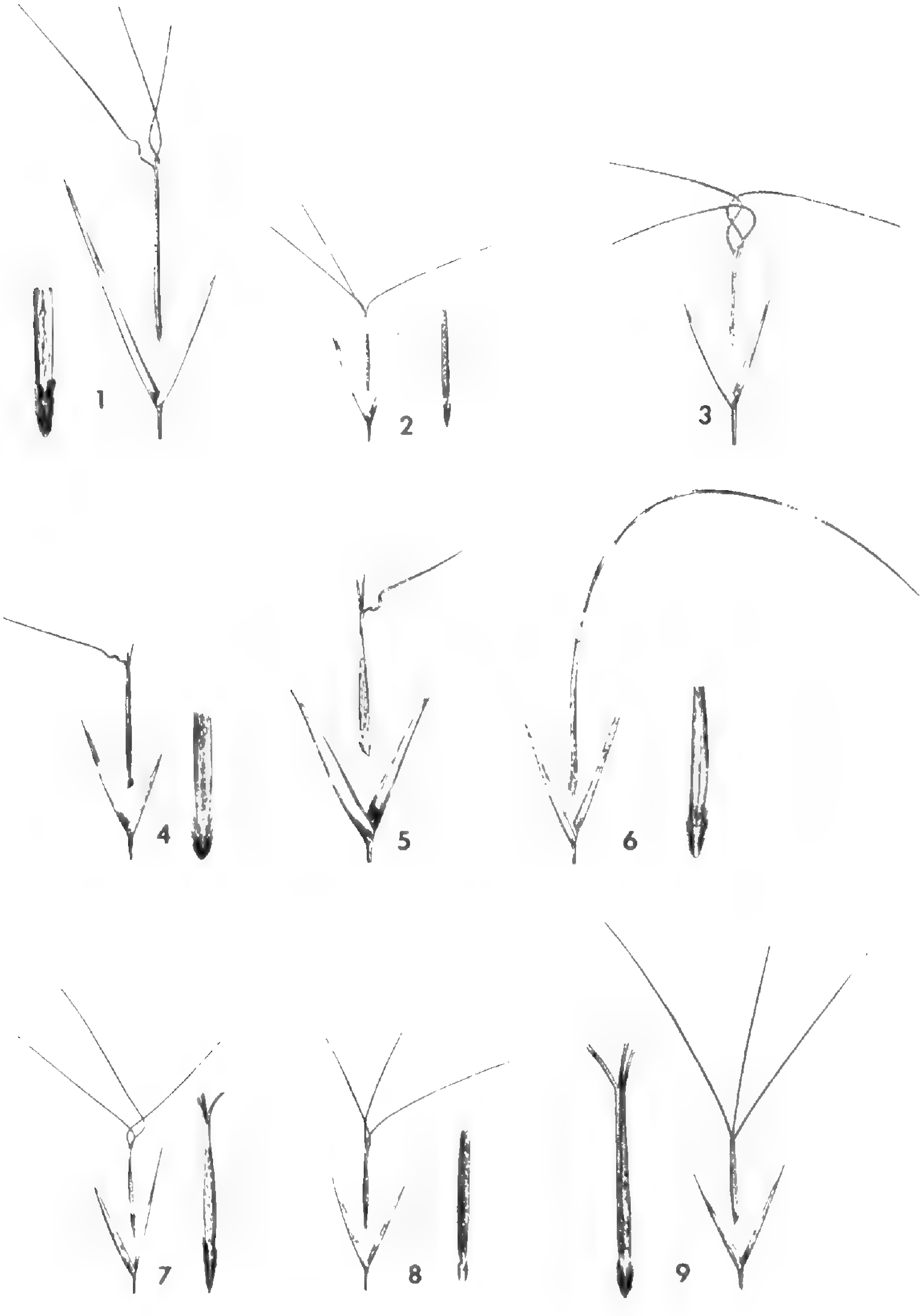
24. Culms usually slender, the lower shoots 1–4 mm broad; panicle branches 1–4 cm long; first glume 1–2 nerved .... (25)

25. Callus 0.4–0.8 mm long.......... **14.** *A. purpurescens*

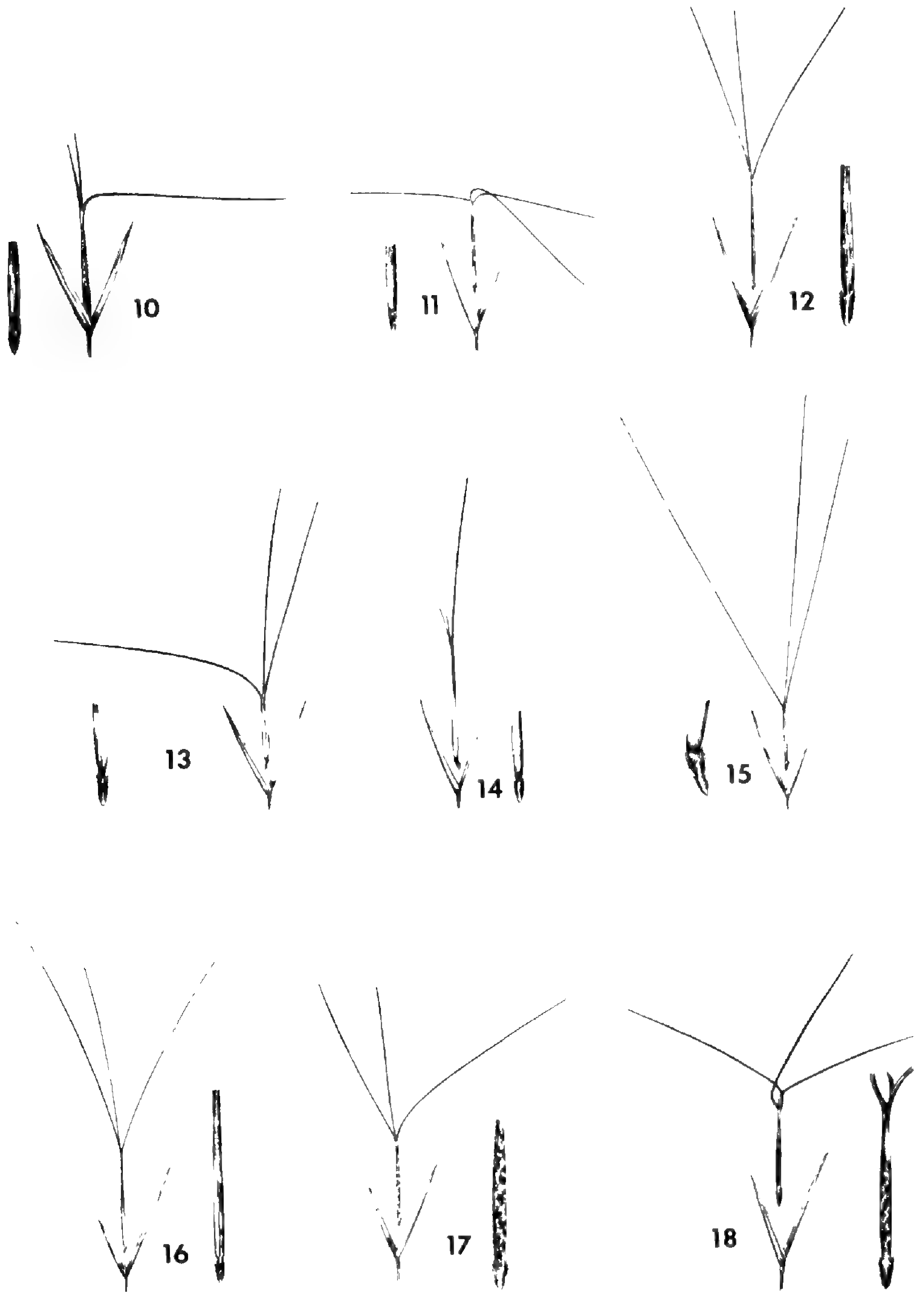
25. Callus 1–2 mm long.................... **6.** *A. gyrans*

1. **Aristida basiramea** Engelm. ex Vasey, Bot. Gaz. 9:76. 1884. Branching annuals to 45 cm tall; panicles narrow and loose, (2) 4–10 cm long; glumes subequal, the first 8–10 mm long, the second 10–12 mm long; lemma about 10 mm long; central awn spirally coiled at base in 2–3 spirals, 10–12 mm long; lateral awns usually spreading, 5–10 mm long. Distribution: Sandy waste places, fields; AL, FL. (Figure 1).

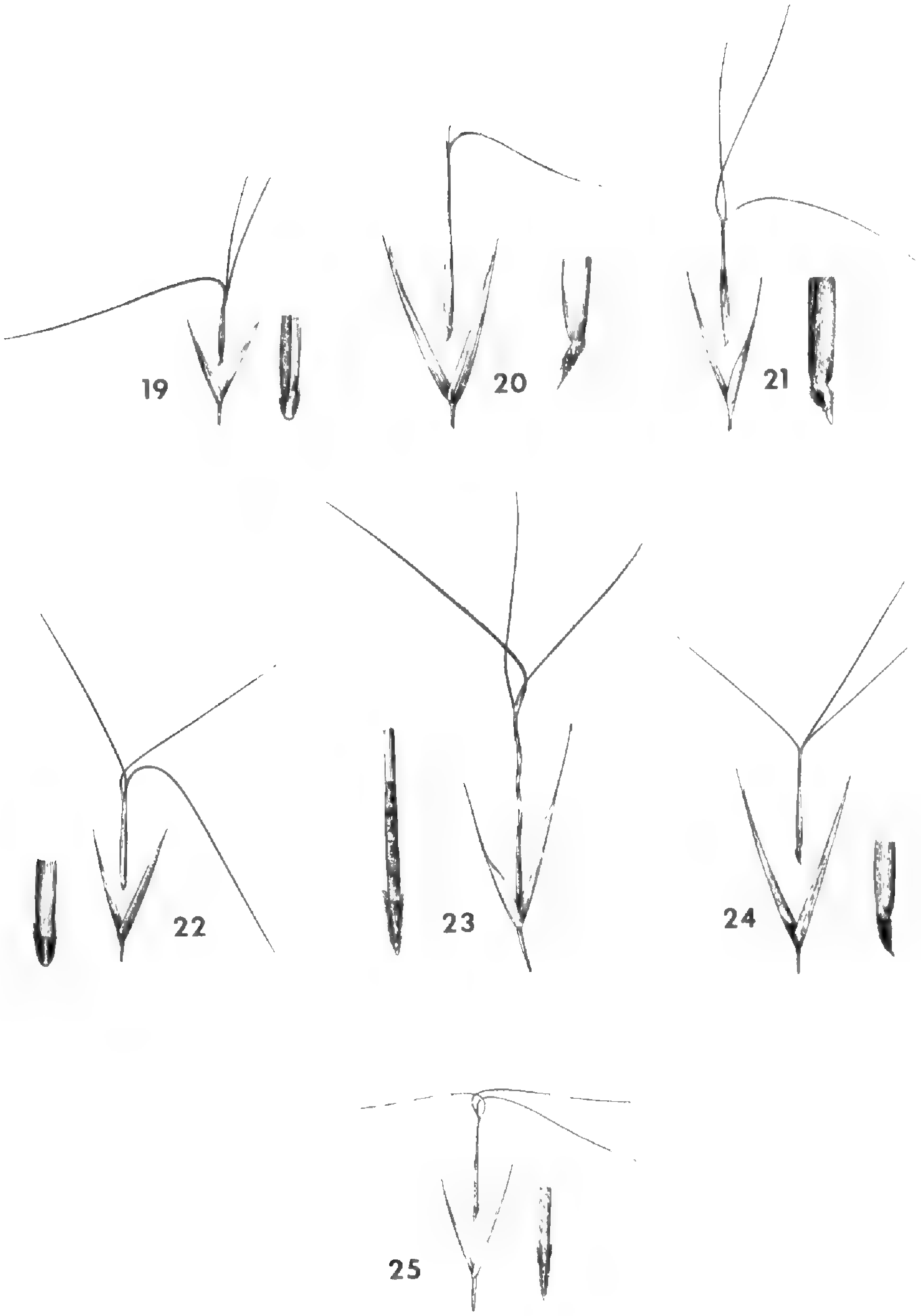
Aristida basiramea grades morphologically into *A. dichotoma* var. *curtissii;* see note under *A. dichotoma.*



Figures 1-9. Spikelets and calluses of *Aristida* of the southeastern United States (from Henrard, 1929, 1932). Approximate scales in parentheses are for spikelet first and callus second. **1.** *A. basiramea* (× 2, 6). **2.** *A. condensata* (× 1.3, 2.6). **3.** *A. desmantha* (× 0.8). **4.** *A. dichotoma* var. *curtissii* (× 1.6, 5.6). **5.** *A. dichotoma* var. *dichotoma* (× 3.2). **6.** *A. floridana* (× 2.4). **7.** *A. gyrans* (× 1.6, 3.2). **8.** *A. lanosa* (× 1, 2.4). **9.** *A. longespica* var. *geniculata* (× 1.6, 4).



Figures 10–18. Spikelets and calluses of *Aristida* of the southeastern United States (from Henrard, 1929, 1932). Approximate scales in parentheses are for spikelet first and callus second. **10.** *A. longespica* var. *longespica* (× 2.8, 4). **11.** *A. mohrii* (× 1, 2.6). **12.** *A. oligantha* (× 0.8, 4). **13.** *A. palustris* (× 1, 2.6). **14.** *A. patula* (× 1, 2.6). **15.** *A. purpurea* var. *longiseta* (× 0.5, 3.2). **16.** *A. purpurea* var. *purpurea* (× 1, 3.2). **17.** *A. purpurescens* var. *purpurescens* (× 1.3, 3.2). **18.** *A. purpurescens* var. *tenuispica* (× 1.3, 3.2).



Figures 19-25. Spikelets and calluses of *Aristida* of the southeastern United States (from Henrard, 1929, 1932). Approximate scales in parentheses are for spikelet first and callus second. **19.** *A. purpurescens* var. *virgata* (× 1.6, 4). **20.** *A. ramosissima* (× 1.2, 4). **21.** *A. rhizomophora* (× 1.2, 4). **22.** *A. simpliciflora* (× 1.6, 5.2). **23.** *A. spiciformis* (× 2, 4). **24.** *A. stricta* (× 1.6, 4.8). **25.** *A. tuberculosa* (× 0.5, 1.6).

2. **Aristida condensata** Chapm., Bot. Gaz. 3:19. 1878. [*A. condensata* var. *combsii* (Scribn. & Ball) Henr.] Erect, robust perennials to 1.5 m tall; sheaths glabrous to pilose, but not lanose; panicles narrow, (15) 20–55 cm long, the branches mostly longer than 4 cm, erect to ascending or slightly spreading; glumes subequal, 6–10 (12) mm long; lemma 6–8 mm long; awns usually contorted at the base, the central 10–15 mm long, the laterals 8–13 mm long. Distribution: Pine savannahs, oak-pine uplands, sandy hills; AL, FL, GA, MS, NC, SC. (Figure 2).

Specimens with glabrous lower sheaths have been recognized as *Aristida condensata* var. *combsii.* There appears to be no geographic or morphologic basis other than pubescence for this variety, and it is submerged within *A. condensata* without formal recognition. *Aristida condensata* is part of the *A. purpurescens* complex and needs to be studied relative to the other entities of this group: *purpurescens, virgata, tenuispica,* and perhaps also *stricta, gyrans, simpliciflora,* and *mohrii.*

3. **Aristida desmantha** Trin. & Rupr., Acad. St. Petersb. Mem. VI. Sci. NAt. 5:109. 1842. Branching annuals to 80 cm tall; sheaths glabrous to pilose-floccose; panicles loose and open, 10–20 cm long, the branches ascending and the spikelets erect; glumes subequal, the body 10–12 mm long with an awn 2-5 mm long, the first slightly longer than the second, lemma 7–10 mm long; awn column 2–5 (7) mm long, articulated with the lemma summit; awns subequal, 2–3 cm long. Distribution: Fields, waste places, dry pine woods; AR, LA. (Figure 3).

Aristida desmantha and *A. tuberculosa* are members of the mostly African section *Arthratherum,* wherein the lemma is terminated by an awn column that breaks from the lemma at maturity. The point of articulation is not always evident, especially in young plants.

4. **Aristida dichotoma** Michx., Fl. Bor. Amer. 1:41. 1803.

First glume as long as or nearly equal to second glume; lemma sparsely appressed-pubescent, 3–8 mm long .... 4a. var. *dichotoma*

First glume 1/2 to 2/3 as long as second glume; lemma glabrous to scaberulous, 6–11 mm long .... 4b. var. *curtissii*

4a. **A. dichotoma** var. **dichotoma.** Plants annual, culms usually much-branched at base; panicles narrow, spikelike 2–11 cm long; glumes subequal, the first 3–6 mm long, the second 4–7 mm long; lemma 3–8 mm long; central awn spirally coiled, 3–6 mm long; lateral awns erect, about 1 mm long. Distribution: Disturbed areas, fields, pine clearings; throughout the region. (Figure 5).

4b. **A. dichotoma** var. **curtissii** A. Gray, Man. Bot. North. U.S. ed. 6. 640. 1890. [*A. curtissii* (A. Gray) Nash; *A. basiramea* Vasey var. *curtissii* (A. Gray) Shinners.] Plants annual, the culms branched at base but less so than in var. *dichotoma;* panicles spikelike 2–11 cm long; glumes unequal, the first 5–8 (10) mm long, the second 7–13 mm long; lemma 6–11 mm long; central awn spirally coiled, 4–8 mm long; lateral awns erect, 2–4 mm long. Distribution: Pine woods, fields, disturbed areas; AL, AR, FL, GA, MD, MS, NC, SC, TN, VA, WV. (Figure 4).

I follow here the treatment of Vaughn (M.S. thesis, Univ. of Oklahoma, Norman, 1981) in relegating *Aristida curtissii* to varietal status under *A. dichotoma.* Vaughn demonstrated the phenetic intermediacy of *A. curtissii* relative to *A. dichotama* and *A. basiramea,* but with greater similarity to *A. dichotoma. Aristida basiramea* seems to be no more distinct from *A. dichotoma* than is var. *curtissii,* and could likewise be treated as a variety of *A. dichotoma.*

5. **Aristida floridana** (Chapm.) Vasey, Grasses U.S. Descr. Cat. 35. 1885. [*A. ternipes* sensu Small, not Cav.] Erect perennials to about 1 m tall, only sparingly branched below; panicles loose, 30–45 cm long, the branches erect to ascending and narrow, or spreading and open; glumes unequal to subequal, the first 10–14 mm long, the second 8–9 mm long; lemma gradually narrowed to a single awn, the midrib prominently thickened, 30–35 mm long from callus to awn tip; central awn gradually curving, sickle-shaped; lateral awns totally lacking or minute points only. Distribution: Roadsides, railroad embankments; FL. (Figure 6).

Aristida floridana is known in the United States only from Key West and Ramrod Key of the Florida Keys, Monroe County. Beetle

(1983) also reported this species from Yucatán, Campeche, and Quintana Roo, Mexico. It is apparently most closely related to *A. ternipes* Cav., a species of the southwestern deserts to central America.

6. **Aristida gyrans** Chapm., Bot. Gaz. 3:18. 1878. Tufted, erect perennials, 20–65 cm tall; sheaths mostly shorter than the internodes, but occasionally longer; blades filiform, involute; panicles narrow, lax, 10–30 cm long; glumes mostly strongly unequal, the first 6–9 (11) mm long, the second 9–12 mm long, some plants with subequal glumes; lemma 6–7 mm long, with an acute prominent callus 0.8–2 mm long; awns subequal, 1–1.5 cm long, somewhat contorted at the base. Distribution: Sandy pinelands, oak scrub; FL, GA. (Figure 7).

The relationships of *Aristida gyrans* are unclear. Even though the glumes are usually strongly unequal, it does not appear to be related to the group *Purpureae,* which are mostly plants of the arid southwest. The callus, awns, and habit suggest an affinity to the *A. purpurescens* complex.

7. **Aristida lanosa** Muhl. ex Ell., Bot. S.C. and Ga. 1:143. 1816. [*A. lanosa* var. *macera* Fern.] Robust, tufted perennials to 1.5 m tall; sheaths longer than the internodes, lanose or floccose, the pubescence occasionally patchy and sparse; panicles narrow, elongate, (25) 35–70 (82) cm long, with tufts of woolly hair at the nodes of the main axis; glumes subequal, the first 8.7–18 mm long, the second 8.4–15 mm long; lemma 6.5–10 mm long; awns unequal, the central 12–28 mm long, the laterals 7–17 mm long. Distribution: Dry fields, pine-oak woods, uplands; throughout the region except KY. (Figure 8).

Although several recent authors have suggested a close similarity of *Aristida lanosa* and *A. palustris,* with some even merging the two taxa, these two species are easily distinguished by both vegetative and spikelet features (Allred, 1985b). *Aristida palustris* lacks lanose sheaths and panicle nodes, and can be distinguished further from *A. lanosa* by having sheaths shorter than the internodes, 2-nerved glumes, longer calluses, and longer awns.

8. **Aristida longespica** Poir. in Lam., Encycl. Sup. 1:452. 1810.

Central awn mostly 1–10 mm long; lateral awns mostly 0–5 mm

long ....8a. var. *longespica*
Central awn mostly 12–27 mm long; lateral awns mostly 6–18 mm long .... 8b. var. *geniculata*

8a. **A. longespica** var. **longespica.** Much-branched annuals; panicles narrow and spikelike; glumes mostly subequal, 2–8 mm long; lemma 2.5–7 mm long; central awn erect to reflexed, 1–10 (14) mm long; lateral awns erect to ascending, 0–5 (8) mm long. Distribution: Disturbed ground, pine and oak woods; throughout the region. (Figure 10).

8b. **A. longespica** var. **geniculata** (Raf.) Fernald. [*A. intermedia* Scribn.] Much-branched annuals, frequently robust and appearing perennial late in the growing season; panicles narrow and spikelike, usually with many spikelets; glumes subequal, 4–11 mm long; lemma 3.5–10 mm long; central awn erect to reflexed, (8) 12–27 mm long; lateral awns erect to horizontal, (1) 6–18 mm long. Distribution: Disturbed ground, pine and oak woods; throughout the region except KY and DE. (Figure 9).

The morphologic similarity of *Aristida longespica* and *A. intermedia* was documented in an earlier paper (Allred, 1985a), justifying the reduction of *A. intermedia* to varietal status. The variety *geniculata* tends to be a more robust plant with larger spikelets and longer awns. Specimens that are intermediate betwen the two varieties are not uncommon; identification of these is difficult and often arbitrary. Nevertheless, because the two extremes are so strikingly different, it seems appropriate to maintain a distinction at the varietal level. Both taxa frequently possess a peculiar banding pattern on the lemma (as does *A. purpurescens* and rarely *A. oligantha* and *A. ramosissima*), but it appears that the expression of this feature is arbitrary and not correlated with any other feature.

9. **Aristida mohrii** Nash, N.Y. Bot. Gard. Bull. 1:436. 1900. Erect, tufted perennials to 110 cm tall; blades of flowering shoots flat, lightly pilose near the ligule; inflorescence 20–45 cm long, unbranched, spicate, the spikelets on very short, stout pedicels on the main axis; glumes subequal, 9–11 mm long; lemma 7–10 mm long;

awns subequal, 1.3–2 cm long, contorted, spreading. Distribution: Sandy pinelands and oak barrens; AL, FL, SC. (Figure 11).

The spicate inflorescences in *Aristida mohrii* and *A. simpliciflora* have led to their frequent confusion with one another. The awns of *A. simpliciflora* are distinctive, with the central about twice as thick as the laterals, whereas in *A. mohrii* the awns are of equal thickness. The two species may also be distinguished by the shorter glumes, lemma, and callus, and less robust habit of *A. simpliciflora.*

10. **Aristida oligantha** Michx., Fl. Bor. Amer. 1:41. 1803. Much branched annuals to 55 cm tall, similar to *Aristida ramosissima;* spikelets often sessile or nearly so; first glume 3–7 nerved, 14–25 mm long; second glume 18–31 mm long, with an awn 7–17 mm long between two setae; lemma 14–20 mm long; central awn 3–7 cm long; lateral awns 2.5–6.0 cm long. Distribution: Waste places, old fields; throughout the region. (Figure 12).

See comments under *Aristida ramosissima.*

11. **Aristida palustris** (Chapm.) Vasey, Grasses U.S. Descr. Cat. 35. 1885. [*A. affinis* of American authors] Stout, tufted perennials to 1.5 m tall; sheaths mostly glabrous, occasionally pilose, mostly shorter than the internodes; panicle narrow, stiff, to 55 cm long; glumes subequal, (7.5) 9–13.5 mm long, the first prominently 2-nerved and 2-keeled; lemma 6–9 mm long; awns unequal, the central 1.5–4 cm long, the laterals 0.8–3.5 cm long. Distribution: Moist ground, marsh and pond shores, lowlands; AL, FL, GA, LA, MS, NC, SC. (Figure 13).

The correct name for this species is not *Aristida affinis* (Schultes) Kunth, as in commonly used; *A. affinis* is the same as *A. purpurescens* and placed in synonymy there (Allred, 1985b). See comments under *A. lanosa* regarding the relationship of *A. palustris* and *A. lanosa.*

12. **Aristida patula** Chapm. ex Nash, Bull. Torr. Bot. Club 23:98. 1896. Erect perennials with short rhizomes, to 1 m tall; panicles 30–50 cm long, loose, open, the branches stiffly spreading to drooping at maturity; spikelets appressed at the ends of the branches; glumes slightly unequal, 10–13 mm long, the first slightly longer than the second; lemma 10–12 (15) mm long to base of awns; central

awn straight, 20–25 mm long; lateral awns 3–10 mm long. Distribution: Roadsides, sandy fields, low pinelands; FL. (Figure 14).

13. **Aristida purpurea** Nutt., Trans. Amer. Phil. Soc. 5:145. 1837.

Summit of lemma 0.3–0.8 mm broad, not gradually narrowed; awns usually stout, 4–10 cm long; second glume 14–25 mm long .... 13b. var. *longiseta*

Summit of lemma 0.1–0.3 mm broad, gradually narrowed; awns slender, mostly 2–6 mm long; second glume mostly shorter than 16 mm .... 13a. var. *purpurea*

13a. **A. purpurea** var. **purpurea.** Tufted perennials 25–60 cm tall; blades involute; panicles loose, the branches usually somewhat drooping; glumes unequal, the first about 1/2 as long as the second; lemma 6–12 mm long, narrow at the summit; awns subequal, (1.5) 2–6 cm long. Distribution: Waste places, roadsides, sandy prairies; AR, LA. (Figure 16).

13b. **A. purpurea** var. **longiseta** (Steud.) Vasey, in Rothr., Rpt. U.S. Survey W. 100th Merid. 6:286. 1878. [*A. longiseta* Steud.] Tufted perennials 12–50 cm tall; blades involute; panicle branches erect and stout to delicate and drooping; glumes unequal, the first about 1/2 as long as the second; lemma 10–16 mm long, broad at the summit; awns subequal, 4–10 cm long. Distribution: Waste places, roadsides; LA. (Figure 15).

A common grass of the plains and deserts of the western United States, *Aristida purpurea* is known only from a few localities in Arkansas and Louisiana. Our plants are best treated at the varietal, rather than the specific level (Allred, 1984b). The variety *longiseta* currently is known only from one collection in St. Tammany Parish, Louisiana, and one from Kershaw County, South Carolina. The record from South Carolina appears to be either an introduction or perhaps an error on the label. Variety *longiseta* was also collected from the Soil Conservation Service Nursery in Chapel Hill, North Carolina.

14. **Aristida purpurescens** Poir. in Lam., Encycl. Sup. 1:452. 1810.

Central awn divaricate to reflexed, about twice as thick at the base as the erect lateral awns .... 14c. var. *virgata*

Central and lateral awns spreading, straight to spirally contorted but not reflexed, and all about the same thickness at the base.

First glume mostly longer than the second; awns straight or slightly contorted at the base; blades 1–3 mm wide, often curling .... 14a. var. *purpurescens*

First glume shorter than or equal to the second; awns spirally contorted at the base; blades about 1 mm wide, usually not curling .... 14b. var. *tenuispica*

14a. **A. purpurescens** var. **purpurescens.** [*A. affinis* (Schulte) Kunth] Tufted perennials to 1 m tall; lower sheaths longer than the internodes, mostly glabrous, occasionally pilose with appressed hairs; blades mostly flat, often curling; panicles narrow, densely to loosely flowered; glumes usually unequal, the first longer than or equal to the second, 6–10 mm long, the second 5–8 mm long; lemma 6–8 mm long; awns 1.5–2.5 cm long, about equal in thickness and angle, usually ascending, the laterals sometimes shorter than the central. Distribution: Waste places, pine savannahs, fields; throughout the region. (Figure 17).

14b. **A. purpurescens** var. **tenuispica** (Hitchc.) Allred, *comb. nov.* Basionym: *Aristida tenuispica* Hitchcock, Contr. U.S. Natl. Herb. 22:581. 1924. Tufted perennial to 1 m tall; sheaths longer or shorter than the internodes, glabrous; blades flat to loosely rolled, mostly not curling; panicles narrow, loosely flowered; glumes subequal, 8–9 mm long, the first equal to or slightly shorter than the second and 1–2 nerved; lemma 6–7 mm long; awns 1.2–1.8 cm long, subequal in thickness, angle, and length, usually spirally contorted at the base. Distribution: Low pine and oak woods, prairies, roadsides; AL, FL, GA, MS, NC, SC. (Figure 18).

14c. **A. purpurescens** var. **virgata** (Trin.) Allred, *comb. nov.* Basionym: *Aristida virgata* Trinius in Sprengel, Neu. Entd. 2:60. 1821. Tufted perennial to 1 m tall; sheaths glabrous, longer or shorter than the internodes; blades flat, curling or not; panicles narrow, densely to loosely flowered; glumes subequal or the first slightly longer, 6–7 mm long; lemma 4–7 mm long; central awn reflexed and about twice as thick at the erect lateral awns, the central 1.3–2 cm long, the laterals 0.8–1.3 cm long. Distribution: Pinelands, oak woods, bogs, waste places, prairies; AL, AR, FL, GA, LA, MS, NC, SC, TN, VA. (Figure 19).

There is significant morphological intergradation among the three entities *purpurescens, tenuispica,* and *virgata,* with spikelets corresponding to more than one entity sometimes present within the same panicle (Allred, 1984a). The lack of a strongly correlated set of features that distinguishes the three taxa prompts their relegation to varieties of a single species. Further studies of chromosome number, breeding behavior, and habitat are needed.

15. **Aristida ramosissima** Engelm. ex Gray, Man. Bot. North. U.S. ed. 2. 550. 1856. [*A. ramosissima* var. *uniaristata* A. Gray; *A. ramosissima* var. *chaseana* Henr.] Much-branched annuals to 60 cm tall, similar to *Aristida oligantha;* spikelets sessile or nearly so; first glume 3-7 nerved, 11–20 mm long; second glume 16–25 mm long, with a short awn 3–7 mm long between two seta; lemmas (8) 14–22 mm long; central awn 9–28 mm long; lateral awns 0–12 (25) mm long. Distribution: Pine savannahs, roadsides, fields; AR, KY, LA, TN. (Figure 20).

The variety *chaseana,* with nearly equal awns, is transitional between this species and *Aristida oligantha,* and perhaps deserves formal recognition. It is usually identified as *A. oligantha.* The variety *uniaristata,* with obsolete lateral awns, is somewhat anomalous in the section *Chaetaria* of *Aristida,* this feature being typical of the section *Streptachne.* Further biosystematic studies of *A. oligantha* and *A. ramosissima* are needed.

16. **Aristida rhizomophora** Swallen, J. Wash. Acad. Sci. 19:196. 1929. Perennials to 100 cm tall, from vigorous rhizomes; old basal sheaths fibrous and shredding into threadlike segments; panicles 20–45 cm long with erect to somewhat flexuous branches; glumes unequal, the first 6–12 mm long including the awn, the second 13–18 mm long including the awn; lemmas 9–13 mm long; awns often arcuate-recurved, the central 15–30 mm long, the laterals 13–20 mm long. Distribution: Sandy pinelands and prairies; FL. (Figure 21).

17. **Aristida simpliciflora** Chapm., Bot. Gaz. 3:18. 1878. Erect, tufted perennials to 80 cm tall; sheaths shorter than the internodes; inflorescence slender, racemose, usually with 2–3 spikelets per node, one short-pedicelled, one long-pedicelled; glumes subequal, 6–8 mm long; lemma 5–6 mm long; central awn strongly reflexed, about twice as thick as the laterals, 1–1.5 cm long; lateral awns spreading to divaricate, 1–1.5 cm long. Distribution: Low dense pine barrens and woods; AL, FL, MS. (Figure 22).

Aristida simpliciflora shows strongest morphologic affinities with *A. mohrii* and *A. purpurescens* var. *virgata.* Awn and panicle features successfully distinguish this species.

18. **Aristida spiciformis** Ell., Bot. S.C. and Ga. 1:141. 1816. Erect perennials to 1 m tall, the culms little-branched; panicles (5) 8–24 cm long, dense and compact, spiciform, with numerous congested spikelets; glumes unequal, the first with a body about 4 mm long and abruptly awned with a 4–12 mm long awn, the second 7–10 mm long and narrowed to an awn 10–12 mm long; lemma 5–6 mm long and terminated by a twisted beak 7–30 mm long; awns mostly subequal, (1) 2–3 cm long, the lateral awns thinner than the central. Distribution: Low pine savannahs, oak woods; AL, FL, GA, MS, NC, SC. (Figure 23).

The dense panicle, awned glumes, and twisted lemma beak are characteristic of the species. Although not developing a zone of articulation and not considered a member of section *Arthratherum,* the lemma beak frequently breaks from the lemma body, presumably from a weakening of the thin lemma tissue above the caryopsis.

19. **Aristida stricta** Michx., Fl. Bor. Amer. 1:41. 1803. Tufted, erect perennials, occasionally with short rhizomes, 45–100 cm tall; blades tightly involute, firm, pilose on the lower (outer) surface near the midrib especially toward the base, also at the collar and throat regions; panicles narrow, 18–35 cm long; glumes about equal, 7–12 mm long; lemma 6–8 mm long; central awn 10–15 mm long; lateral awns 10–13 mm long. Distribution: Pinelands, sandy fields; AL, FL, GA, MS, NC, SC. (Figure 24).

Herbarium specimens of this species almost always show charred plant bases.

20. **Aristida tuberculosa** Nutt., Gen. Pl. 1:57. 1818. Branching annuals to 1 m tall; panicles 10–20 cm long, loose with somewhat stiff, ascending branches; spikelets erect, yellowish-brown; glumes subequal, 20–30 mm long, the second slightly longer than the first, gradually acuminate and awned; lemma 10–14 mm long from callus to point of articulation with the column; awn column 8–15 mm long, breaking at maturity; awns subequal, 3–4 cm long. Distribution: Sandy fields, pinelands, disturbed areas; AL, FL, GA, MD, MS, NC, SC, VA. (Figure 25).

The spikelets (glumes, lemma, awns) in *Aristida tuberculosa* are generally larger than in *A. desmantha.* In both, the awn column is formed by the connivent awn bases, frequently twisted in *A. tuberculosa,* and not formed by the narrowing of the lemma apex.

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DEPARTMENT OF ANIMAL AND RANGE SCIENCES
BOX 3 - I, NEW MEXICO STATE UNIVERSITY
LAS CRUCES, NM 88003

NOMENCLATURAL NOTES ON *HEDYOTIS ROSEA* RAFINESQUE AND A NEW COMBINATION IN *HOUSTONIA*[1]

EDWARD E. TERRELL

ABSTRACT

The nomenclatural application of the name *Hedyotis rosea* Rafinesque (1817) is discussed. It is concluded that the name applies to the species also known as *Houstonia pygmaea* C. H. & M. T. Muller (1936). The new combination, *Houstonia rosea* (Rafinesque) Terrell, is proposed and a neotype is designated.

Key Words: *Hedyotis, Houstonia,* Rubiaceae, nomenclature

Hedyotis rosea Rafinesque (1817) and *Houstonia pygmaea* C. H. and M. T. Muller (1936) are two competing names for a diminutive early spring-flowering rubiaceous annual that occurs in the southeastern and southcentral United States. The protologue of *Houstonia pygmaea* describes the species quite adequately, as it includes a detailed description in English with a rather full Latin diagnosis, comments on habitat, distinguishing characters, and citations of type specimens. The name *Hedyotis rosea* Raf. was first adopted by Waterfall (1953) and later used by Lewis (1970) in his treatment of *Hedyotis* for the "Manual of Vascular Plants of Texas." The protologue is very brief and application of the name tenuous. The following discussion takes up in detail the question of whether this name referred to the same species as *Houstonia pygmaea.*

Rafinesque (1817) described *Hedyotis crassifolia* (*Houstonia pusilla*) and *Hedyotis rosea* as follows:

"243. *Hedyotis crassifolia* Raf. Ramis tenuis divaricatis sulcatis unifloris, foliis sessilibus oblongis acutis glabris integris carnosis, floribus longe pedunculatis. Raf.—Anonyme 1. Rob. p. 454. This plant although resembling very much the *Houstonia,* is a real *Hedyotis* having a capsul two celled and polysperme. It blossoms in February, it varies with white, deep violet and pale violet flowers, stem only two inches high, tube of the corolla filiform, four stamina

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in the tube nearly sessile, style short, stigma oblong, capsul heart shaped, with many minute seeds.

"244. *Hedyotis? rosea* Raf. Repens, floribus roseis Anonyme 2. Rob. p. 454. This may be the *Houstonia tenella* of Lyon and Pursh; Robin does not describe it, but he merely says it is still smaller than the foregoing, creeping, and with flowers of a pale rose colour."

Rafinesque's "Florula Ludoviciana" (1817) was a translation from the French of "Flore Louisianaise," the third volume of an account by Claude C. Robin (1807) of a journey in western Florida, Louisiana, and parts of the West Indies. Rafinesque's florula was more than a translation, however, but a new work, providing binomials for the taxa lacking binomials in Robin's book (Merrill, 1949; Ewan, 1967).

It is desirable to find out whether Robin's original description, from which Rafinesque's protologue was taken, provides additional information about the identity of *Hedyotis rosea.* Robin described the plants in French, adding a Latin genus name or approximation to a genus name. For the plants in question Robin described three unnamed species under the general heading "Garance (rubia)." The first species was in 1817 named *Rubia techensis* Raf., possibly a species of *Galium* (Merrill, 1949). The description of the second species was faithfully translated by Rafinesque, who named it *Hedyotis crassifolia.* The third species, *H. rosea* Raf., was described as follows:

"Une autre plus petite, se trainant et traçant davantage, porte des fleurs rose tendre: elles pourraient, au printemps, émailler agréablement des compartimens de parterres ou de gazons.

"Ces espèces paraissent se rapprocher de l'*oldenlandia*, si ce n'est que le tube de la corolle est très-alongé, tandis que l'*oldenlandia* est à peine tubulé."

In their descriptions, Robin and Rafinesque provided four characteristics for *Hedyotis rosea:* (1) plants smaller than those of *H. crassifolia,* (2) flowers pale rose, (3) corolla tubes longer than those of *Oldenlandia* species, and (4) plants creeping. It is necessary not only to determine what species best fits this brief description, but also to know the identity and characteristics of *Hedyotis crassifolia,* as *Hedyotis rosea* was directly compared to it.

Hedyotis crassifolia Raf. was adequately described and has been generally accepted (e.g., Lewis, 1970) as referring to the species also known as *Houstonia pusilla* Schoepf or *H. patens* Elliott, the common "small bluets" of the southeastern states, ranging from northern Maryland (where adventive) to northwest Florida, west to Texas, and north to Illinois. It has the following characteristics: (1) plants 1.5–20 (usually 5–15) cm. tall, (2) corollas usually purple with reddish centers, but varying to violet, lavender, pink, or white with yellow centers (various color forms sometimes occur in a single population), (3) corolla tubes 2–5 mm long, and (4) plants erect or spreading.

The characteristics of *Houstonia pygmaea* (=*Hedyotis rosea*?) are: (1) plants 1–4 (–5) cm. tall), (2) corollas varying from white to pale pink or pale rose, (3) corolla tubes 3.5–6 mm long, and, (4) plants erect, spreading, or sprawling. It is apparent that three of the four described characteristics of *Hedyotis rosea* apply to *Houstonia pygmaea:* the latter is smaller than *Hedyotis crassifolia;* it usually has pale rose or pale pink flowers (along with some white flowers); and it and *H. crassifolia* have elongate corolla tubes compared to the rotate or short-tubular corollas of *Oldenlandia boscii* (DC.) Chapman, *O. uniflora* L., and *O. corymbosa* L., the three commonest *Oldenlandia* species present in the Gulf Coastal Plain. The fourth characteristic, however, does not agree. In reference to the creeping habit, Rafinesque speculated that *Hedyotis rosea* could be the same as *Houstonia tenella* Pursh, but the latter is now known to be a synonym of the very different species, *H. serpyllifolia*, centered in the southern Appalachians. To find out exactly what Robin may have meant by "se trainant et traçant davantage," I requested a translation from Smithsonian botanist Dr. Marie-Hélène Sachet. She translated it literally as "'dragging itself' and creeping," and commented that "What is meant is that the plant is completely prostrate, with stems running along the ground, like stolons."

Are there any creeping taxa in the southeastern states that have the characteristics of *Hedyotis rosea*? Two creeping rubiaceous species exist there. *Houstonia procumbens* is creeping, but almost invariably has white flowers and is not necessarily smaller than *H. pusilla* (*Hedyotis crassifolia*). It usually has broadly ovate or suborbicular leaves, in considerable contrast to *Hedyotis crassifolia*. It occurs in southeastern Louisiana east to Florida, Georgia, and South Carolina. Another species, *Oldenlandia salzmannii,* is an accidental introduction from South America; it was recently discovered near Pensacola, Florida, and in adjacent Alabama (Fosberg and Terrell, 1985). It is creeping and has pink or light purple flowers. Its corolla tubes are longer than those of most *Oldenlandia* species, but relatively shorter and distinctly wider than those of the houstonias. It is known that Robin visited Pensacola, but unlikely that this supposedly recent introduction was present there at that time.

Could *Hedyotis rosea* have referred to a pink variant of *H. crassifolia*? This conclusion is doubtful as pink flowers are scarce in *H. crassifolia* and when present would often be accompanied by other color variants in the same population. Furthermore, plants of *H. crassifolia* are commonly larger, as noted previously.

That *Hedyotis rosea* was based on a species not in the Rubiaceae seems unlikely because of Robin's supplemental description (omitted by Rafinesque) regarding the occurrence of elongated corolla tubes in both *H. crassifolia* and *H. rosea.* This omission seems to point to a close relationship between these two species and excludes from consideration many non-rubiaceous herbs in the Louisiana flora. I asked Dr. R. Dale Thomas, who has collected extensively in Louisiana, whether he knew of any other herb besides *Houstonia pygmaea* that fits the description of *Hedyotis rosea,* and his reply was negative. To this I would add that the combination of pale rose tubular corollas on consistently very small plants is unusual.

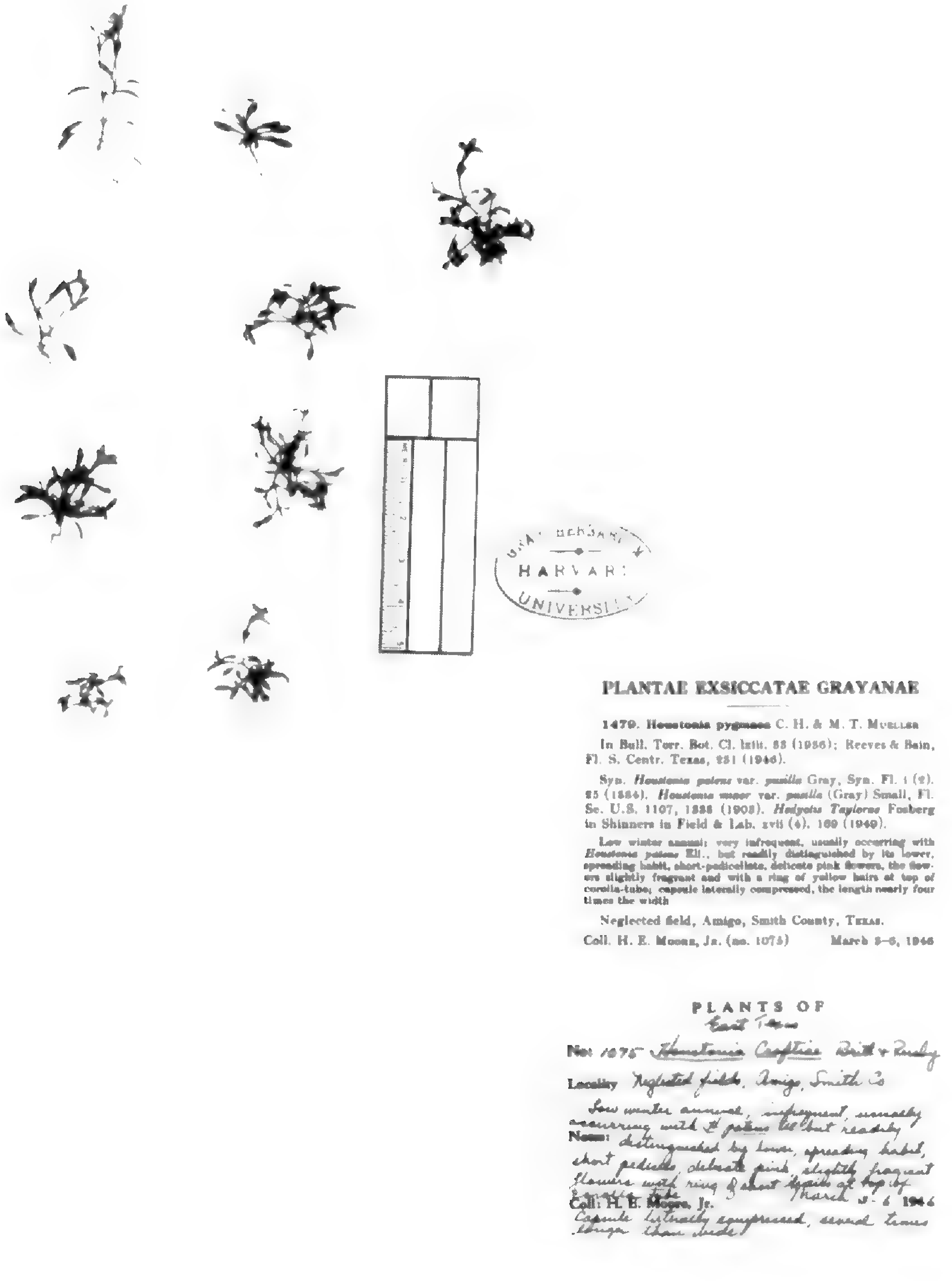
Neither Robin nor Rafinesque cited specimens or locations for *Hedyotis crassifolia* and *H. rosea.* For *Rubia techensis* Raf. the name Teche was mentioned, referring to the bayou Teche in southern Louisiana. Mentioned by Robin and Rafinesque are the Ouachita region, the Red River (flows north to south through Louisiana), and New Orleans. It is also known that Robin visited the Opelousas area in southern Louisiana, and Natchez, Mississippi (J. Ewan, pers. comm.). At present, *Houstonia pusilla* (*Hedyotis crassifolia*) is very common and widespread in Louisiana. *Houstonia pygmaea* is less common, but occurs in at least 24 parishes throughout the state except the extreme south. It occurs in St. Landry Parish, which includes the city of Opelousas. Accordingly, it seems likely that Robin could have come across plants of this species.

Waterfall (1953), in taking up *Hedyotis rosea,* discussed in some detail Rafinesque's description of *Hedyotis rosea,* but he did not refer back to Robin's work. He emphasized that the rose color of the flowers is striking and distinctive, and also stated that the species "is not repent with us (it appears so in some well developed specimens)." Waterfall went on to state his opinion that despite the brief protologue, Rafinesque "*did* furnish it with a description that seems to characterize it. Can it, then, be rejected as a *nomen dubium*?"

In summary, three out of four characteristics of *Hedyotis rosea* agree with those of *Houstonia pygmaea.* Furthermore, the latter species occurs over most of Louisiana and certainly in some of the areas traversed by Robin. The only discordant item in the description of *Hedyotis rosea* is the creeping characteristic which translated literally suggests a stoloniferous or trailing species. Should we reject the name *Hedyotis rosea* as a nomen dubium on the grounds that Robin meant quite literally creeping and was, therefore, referring to some other species than *Houstonia pygmaea*? Is it easier to make a mistake regarding flower color than to err as to creeping?

The weight of the evidence given above leads me to accept the name *Hedyotis rosea* as the same as *Houstonia pygmaea.* It *is* possible that Robin saw massed plants of the tiny annual and supposed without close observation that they were creeping, or that he made some kind of observational error. Also, his brief description in contrast to that of *Hedyotis crassifolia* suggests that he may not have been very familiar with a species so casually described. The acceptance of the name also agrees with usage established by Lewis (1970) in the manual of the Texas flora.

Rafinesque (1817) based his descriptions solely on those of Robin (1807), as there are no extant specimens of Robin's (see Stafleu and Cowan, 1983); therefore, it is advisable to designate a neotype. A neotype was selected by me from a collection widely distributed to a number of herbaria: *H. E. Moore, Jr. 1075* from Texas, distributed as *Plantae Exsiccatae Grayanae 1479* under the name *Houstonia pygmaea* (Moore originally labelled it *H. croftiae* Britton & Rusby). It so happens that the neotype (GH) shows sprawling plants (Figure 1); could such plants as these have led Robin to use the word creeping?



PLANTAE EXSICCATAE GRAYANAE

1470. Houstonia pygmaea C. H. & M. T. Mueller

In Bull. Torr. Bot. Cl. lxiii. 33 (1936); Reeves & Bain, Fl. S. Centr. Texas, 231 (1946).

Syn. *Houstonia patens* var. *pusilla* Gray, Syn. Fl. i (2). 25 (1884). *Houstonia minor* var. *pusilla* (Gray) Small, Fl. Se. U.S. 1107, 1338 (1903). *Hedyotis Taylorae* Fosberg in Shinners in Field & Lab. xvii (4). 109 (1949).

Low winter annual; very infrequent, usually occurring with *Houstonia patens* Ell., but readily distinguished by its lower, spreading habit, short-pedicellate, delicate pink flowers, the flowers slightly fragrant and with a ring of yellow hairs at top of corolla-tube; capsule laterally compressed, the length nearly four times the width

Neglected field, Amigo, Smith County, Texas.

Coll. H. E. Moore, Jr. (no. 1075) March 5–6, 1946

PLANTS OF
East Texas

No: 1075 Houstonia Croftiae Britt & Rusby

Locality Neglected fields, Amigo, Smith Co

Notes: Low winter annual, infrequent, usually occurring with H. patens Ell. but readily distinguished by lower, spreading habit, short pedicels, delicate pink, slightly fragrant flowers with ring of short hairs at top of corolla tube. Capsule laterally compressed, several times longer than wide.

Coll: H. E. Moore, Jr. March 5-6 1946

Figure 1. Neotype of *Houstonia rosea* (Raf.) Terrell.

Generic delimitations among *Hedyotis*, *Houstonia*, and *Oldenlandia* were discussed by Terrell (1975) and are under further study. It is questionable whether any of the North American species referred to *Houstonia* or *Hedyotis* are closely related to *Hedyotis* *fruticosa* L., the type species, a native of Sri Lanka. Although taxonomic relationships of *Houstonia rosea* within *Houstonia* are ambiguous, it seems best to relate the species tentatively to other early spring-flowering bluets with similar habits. These true bluets are in the *H. caerulea* group, including *H. caerulea* L. (the type species); *H. serpyllifolia* Michaux [*Hedyotis michauxiana* Fosberg]; *Houstonia pusilla* Schoepf [*H. patens* Elliott; *Hedyotis crassifolia* Raf.; *Houstonia minima* Beck]; *H. micrantha* (Shinners) Terrell [*Hedyotis australis* W. H. Lewis & D. M. Moore]; and *H. procumbens* (Walter ex J. F. Gmelin) Standley [*Hedyotis p.* (Walter ex J. F. Gmelin) Fosberg]. The base chromosome number for this group is $x = 8$, except for *H. procumbens* with $n = 7$ (Lewis, 1962). *Houstonia rosea* has $n = 7$ (Lewis, 1962), but is not very closely related to *H. procumbens,* judging by reproductive morphology. Pollen of *H. rosea* is similar to but smaller than that of other members of the *H. caerulea* group (Lewis, 1965). Seeds of *H. rosea* are more or less cymbiform with an elongate hilar ridge in a ventral depression, thus they resemble seeds of the *H. rubra* Cav. and *H. purpurea* L. groups rather than the subglobose seeds of *H. caerulea* and its close relatives. Although seed morphology is very important in *Houstonia* and allied genera, it is difficult in this instance to ignore the chromosome number, which agrees with the *H. caerulea* group rather than with the *H. rubra* group ($x = 11$) and *H. purpurea* group ($x = 6$).

The new combination and synonymy are given below. In the absence of a type specimen for *Houstonia rosea,* a neotype is designated, following ICBN, Art. 7.4, 7.8, and T5 (Voss et al., 1983).

Houstonia rosea (Rafinesque) Terrell, *comb. nov.*

Hedyotis rosea Rafinesque, Florula Ludoviciana 77. 1817. NEOTYPE, here designated: Texas. Smith Co.: neglected field, Amigo, 3–6 March 1946, *Moore 1075,* distributed as *Plantae Exsiccatae Grayanae 1479* (as *Houstonia pygmaea*); NEOTYPE GH!; ISONEOTYPES DUKE!, MO!, NCSC!, NO!, NY!, US!, and others.

Houstonia patens Elliot var. *pusilla* A. Gray, Syn. Fl. N. Am. 1, 2: 25. 1884. LECTOTYPE: Louisiana. Rapides Parish: Alexandria, *Hale s.n.* (GH!) (lectotype designated by W. H. Lewis, Ann. Missouri Bot. Gard. 55: 31–33. 1968).

Houstonia pygmaea C. H. & M. T. Muller, Bull. Torrey Bot. Club 63: 33–34. 1936, non *Hedyotis pygmaea* Roemer & Schultes, Syst. Veg. 3: 526. 1818. (= *Houstonia wrightii* A. Gray). SYNTYPES: Texas. Dewitt Co.: 16 Feb and 6 Mar 1934, *Muller 3* and *4*, specimens originally deposited in Muller herb. at Cuero, Texas, and "cotypes" at NY, but present locations unknown, as NY now has no types of this species. Another specimen by same collectors, but not cited as a type: Texas. Dewitt Co.: Mission Valley, 11 Feb 1934, *Muller 1* (GH!).

Hedyotis taylorae Fosberg, in Shinners, Field and Lab. 17: 169. 1949.

Hedyotis minima (Beck) Torrey & Gray f. *albiflora* Lathrop, Rhodora 59: 95. 1957. HOLOTYPE: Kansas. Woodson Co.: Sec 32, T25S, R15E, *Lathrop and McGregor 35* (KANU) (fide W. H. Lewis, Ann. Missouri Bot. Gard. 55: 31–33. 1968). (Note: *Hedyotis minima* f. *minima* (*Houstonia minima* Beck) = *Houstonia pusilla* Schoepf sens. lat.).

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DEPARTMENT OF BOTANY
UNIVERSITY OF MARYLAND
COLLEGE PARK, MARYLAND 20742

TAXONOMY OF *CAREX* SECTION *FOLLICULATAE* USING ACHENE MORPHOLOGY

Daniel E. Wujek and Francis J. Menapace

ABSTRACT

Scanning electron microscopy was used to examine the surfaces of achenes of *Carex* section *Folliculatae* and the allied section *Collinsiae* for systematic relationships. Epidermal patterns were distinctive and consistent for each taxon. Variation of epidermal cells was most evident with respect to size of cell, the number, thickness, and sinuosity of anticlinal walls per cell, and shape of the apex of silica bodies present in two of the taxa. Recognition of *Carex lonchocarpa* is supported.

Key Words: *Carex*, systematics, achene, Cyperaceae, SEM, EDS

INTRODUCTION

Carex folliculata is one of three taxa traditionally placed within the section *Folliculatae*. Mackenzie (1935) recognized three distinct species (*C. folliculata* L., *C. michauxiana* Boeckl., and *C. lonchocarpa* Willd.). Other authors (e.g., Small, 1933; Fernald, 1950; Gleason, 1952; Gleason & Cronquist, 1963; Radford, Ahles & Bell, 1968; Correll & Correll, 1975; Godfrey & Wooten, 1979) also treat this group in their floras as being composed of three taxa (Table 1), but recognize *C. folliculata* var. *australis* Bailey in synonymy of *C. lonchocarpa*.

The members of this group have not been critically reviewed since their original descriptions. This study was initiated to investigate the *Carex folliculata* aggregate and the closely allied section *Collinsiae* in eastern North America. Scanning electron microscopy (SEM) of achene characteristics was utilized in the study. Our findings (Tallent and Wujek, 1983a, 1983b; Menapace and Wujek, 1985) confirm those of earlier studies by Walter (1975), Toivonen and Timonen (1976) and Standley (Ph.D. thesis, Univ. of Washington, Seattle, 1981; 1985) that achene epidermal characteristics provide criteria useful for delimitation of taxa at various levels.

MATERIALS AND METHODS

Perigynia containing mature achenes of all species and varieties of *Carex* sections *Folliculatae* and *Collinsiae* were taken from herbarium specimens deposited at the University of Michigan. Collection

Table 1. Collection data for *Carex* species used for SEM observations.

Section *Folliculatae*
  C. folliculata L.
    Ohio: *Bissell 228;* Indiana: *Lyon* (*s.n.*); Mass.: *Fogg 443*; Canada (Ont.): *Brunton 4289*
  C. lonchocarpa Mackenzie
    North Carolina: *Ahles 45925*; Mississippi: *Tracy 4830*
  C. michauxiana Boeckl.
    Vermont: *Grout 662, Ball 1426;* Canada (Que.): *Roy 535*; (Ont.): *Grassel 4374*, Meyer *11321*

Section *Collinsiae*
  C. collinsii Nutt.
    New Jersey: *Hermann 3213, Canby* (*s.n.*); Georgia: *Ashe 287*

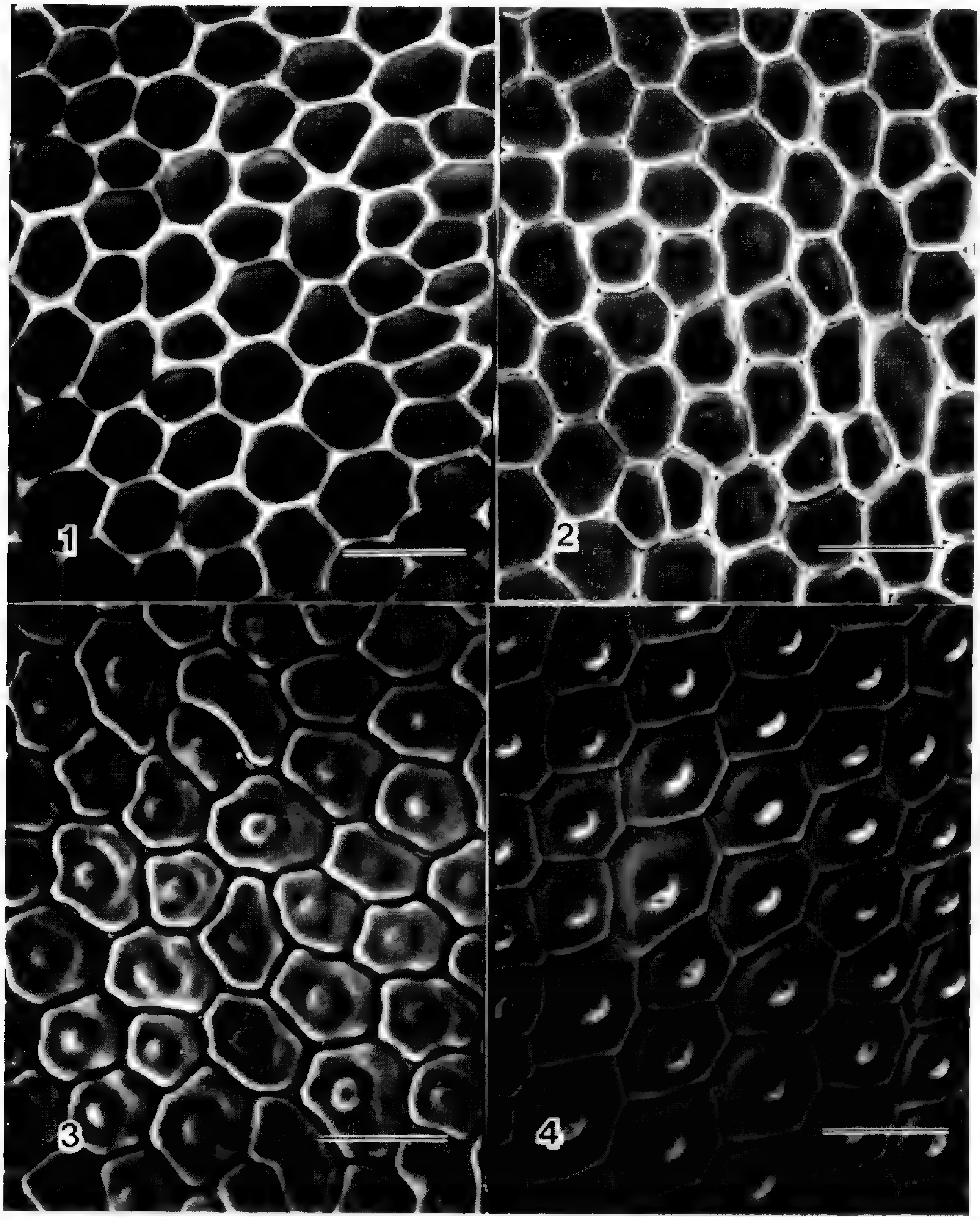
data for SEM studies are given in Table 1. Achenes were dissected out of the perigynia and subjected to a cleaning procedure of sonification, followed by soaking for 18–36 hrs. in a 1:9 concentrated sulfuric acid: acetic anhydride solution. This latter step, modified from Walter (1975), is essential to remove the outer walls of epidermal cells for examination of silicon ornamentations. Achenes were then rinsed in distilled water and desiccated prior to sputter coating with 30 nm of gold. Two or three achenes of each plant were examined by an AMR 1200 SEM and photographed using Polaroid P/N 665 film.

Qualitative x-ray spectra of the epidermal cells were obtained with an energy-dispersive spectrometer (EDS; Ortec 5000) attached to a Hitachi S 520 SEM. Beam accelerating voltage was maintained at 15 kV.

OBSERVATIONS AND DISCUSSION

Features of the achene surfaces are constant within species, even in herbarium specimens up to 50 years old. Among the species, achene epidermal cells ranged from apparent lack of silica bodies [*Carex folliculata* (Figure 1), *C. michauxiana* (Figure 2)] through the presence of central silica bodies [*C. lonchocarpa* (Figure 3), *C. collinsii* (Figure 4)].

A typical achene for these sections has epidermal cells with four to eight anticlinal (radial) walls that are generally sinuous, but may be straight in some taxa (*Carex folliculata, C. collinsii*). A single or double hemispherical body (Figures 3, 4) arising from the inner



Figures 1–4. SEM photographs of *Carex* achenes. **1.** *C. folliculata.* **2.** *C. michauxiana.* **3.** *C. lonchocarpa.* **4.** *C. collinsii.* Scale bar = 40 μm

periclinal wall of the epidermal cells is smooth apically and not nodulose as has been reported in other *Carex* taxa (Menapace, M.S. thesis, Central Mich. U., Mt. Pleasant, 1985). X-ray spectrometry confirmed that the major element in the hemisphere body is silicon, of which the chemical form in these plants is silica.

In *Carex folliculata* (Figure 1), each achene epidermal cell is nearly as wide as long, and generally has straight anticlinal walls and a smooth platform that lacks a central body.

The epidermal pattern of *Carex michauxiana* (Figure 2) is most similar to that of *C. folliculata* in terms of overall size and morphology of cells. The silica platform does not, however, extend to the anticlinal wall but possesses a rounded margin producing a narrow wing toward the base of the achene.

Each epidermal cell of *Carex lonchocarpa* (Figure 3) has sinuous anticlinal walls and one, occasionally two, central bodies. Platforms are flat except for being concave at the base of each central body.

The achene epidermal cells of *Carex collinsii* (Figure 4) usually have five straight anticlinal walls. Each platform possesses a single central body with a buttress which is less concave than that observed in *C. lonchocarpa*.

The epidermal patterns of the achene surfaces can be used to differentiate the taxa in the sections *Folliculatae* and *Collinsiae*. Studies of achene surfaces in other groups of Cyperaceae, particularly in *Scirpus* and *Eriophorum* (Schuyler, 1971), *Cyperus* (Denton, 1983), and in *Carex* (Walter, 1975; Toivonen & Timonen, 1976; Standley, Ph.D. thesis, U. of Washington, Seattle, 1981, 1985; Tallent & Wujek, 1983a, 1983b; Menapace, M.S. thesis, Central Mich. U., Mt. Pleasant, 1985; Menapace & Wujek, 1985) have shown the usefulness of achene epidermal studies in the elucidation of species relationships.

In section *Folliculatae* and *Collinsiae*, the most distinctive epidermal patterns are those of *Carex lonchocarpa* and *C. collinsii*, both of which have prominent silica central bodies with conspicuous buttresses. The nature of the central body in these two taxa appears to reflect convergence. They differ, however, in many other aspects of their overall morphology (Mackenzie, 1935).

Apart from showing exclusive or distinctive achene micro-morphological characters, all four taxa are distinguishable from each other. The gross morphology of *Carex folliculata* and *C. lonchocarpa*, substantiated by achene micromorphology, supports Mackenzie's (1935) recognition of the two taxa at the species level.

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DEPARTMENT OF BIOLOGY
CENTRAL MICHIGAN UNIVERSITY
MT. PLEASANT, MI 48859

CAREX STRIATA, THE CORRECT NAME FOR *C. WALTERIANA* (CYPERACEAE)

A. A. Reznicek and P. M. Catling

In 1893, Liberty Hyde Bailey proposed the name *Carex walteriana* to replace the then familiar *C. striata* Michaux for a widespread coastal plain species ranging from Massachusetts to Florida and Alabama. This name was a replacement because of the existence of a prior *C. striata* Gilibert (1792). Bailey's name has gained universal acceptance in North American floras (Small, 1933; Mackenzie, 1935; Fernald, 1950; Gleason, 1952; Gleason & Cronquist, 1963; Radford, Ahles, and Bell, 1964).

As pointed out by Hylander (1945) and McVaugh (1949), and noted again by Crins (1985), Gilibert (1792) did not consistently use the Linnaean binary system of nomenclature. The binomials in Gilibert's work are thus not validly published under art. 32.1(b), for his "epithets" are not to be treated as epithets (see art. 23 ex. 11) (Voss, et al., 1983). Later use of such binomials does not create homonyms. Michaux's *Carex striata,* therefore, is not a later homonym, but rather the earliest correct name for the species now known as *C. walteriana.*

Carex striata Michaux, Fl. Bor.-Amer. 2: 174. 1803—Holotype: "Hab. in Carolina," *Michaux* (P, IDC microfiche 6211:110 MICH!)

Carex walteriana L. Bailey, Bull. Torrey Bot. Club 20: 429. 1893. Based on *C. striata* Michaux.

Plants of *Carex striata* from South Carolina southward normally have more or less pubescent perigynia. Plants occurring from South Carolina northward supposedly have glabrous perigynia. Michaux's type has pubescent perigynia and the glabrous, northern plants have been segregated as *C. striata* var. *brevis* L. Bailey [*C. walteriana* var. *brevis* (L. Bailey) L. Bailey] (Bailey, 1889, 1893).

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A. A. R.
UNIVERSITY OF MICHIGAN HERBARIUM
NORTH UNIVERSITY BLDG.
ANN ARBOR, MICHIGAN 48109

P. M. C.
BIOSYSTEMATICS RESEARCH INSTITUTE
AGRICULTURE CANADA
WM. SAUNDERS BLDG., C. E. F.
OTTAWA, ONTARIO
CANADA K1A 0C6

NEW ENGLAND NOTES

REDISCOVERY OF *ISOTRIA VERTICILLATA* (WILLD.) RAF. (ORCHIDACEAE) IN VERMONT

MICHAEL EFFRON AND ERROL C. BRIGGS

The large whorled pogonia (*Isotria verticillata*) is at the northern limits of its range in northern New England, and is considered an endangered species in Maine, New Hampshire, and Vermont (Crow et al., 1980). In these three states, this orchid is less frequently found than the other member of the genus, the federally listed *Isotria medeoloides* (Pursh) Raf.

Isotria verticillata has been reported from two stations in Maine in this century. The most recent report was from Waterford in 1974 (Campbell and Eastman, 1980). Brackley (1985) reported only one extant populatión in New Hampshire.

Documented stations for this orchid in Vermont include a collection by Benedict in the 1840's "at the High Bridge" in Colchester, collections in Pownal (1897), in Bristol (1898), and a number of collections in Burlington and Colchester in 1902, 1903, and 1904. During the last 81 years, the species has not been reported from Vermont, leading the committee currently revising the state's endangered species list to assume it was extirpated in the state.

A vigorous population of *Isotria verticillata* was discovered on June 4, 1985 in the town of Colchester (Chittenden County), several miles from Benedict's station. The orchids grow in a level forest of middle-aged *Acer rubrum, Quercus rubra* and *Q. alba,* with occasional *Pinus Strobus.* Understory trees and shrubs include *Acer pensylvanicum, Ostrya virginiana, Hamamelis virginiana, Kalmia angustifolia, Vaccinium vacillans, Viburnum acerifolium,* and *Corylus cornuta.* The herbaceous community contains *Maianthemum canadense, Medeola virginiana, Trientalis borealis, Aralia nudicaulis,* and *Pteridium aquilinum.* Names follow Fernald, 1950.

The population of *Isotria verticillata* at this station can be conservatively estimated at over 1000 stems, and the species is the predominant herbaceous plant at many sites in the area. The number of plants and the apparent vigor of the colony is in keeping with the occurrence of the species in more southerly parts of its range. With the exception of an unvouchered account of *I. verticillata* from

Aroostook County, Maine (Goodale, 1861), however, these plants represent the northernmost station for either species of *Isotria*.

Specimens (*Effron 0051*) have been deposited at VT and NEBC.

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AQUATEC, INC.
ENVIRONMENTAL SERVICES
75 GREEN MOUNTAIN DRIVE
SOUTH BURLINGTON, VT 05401

NEW STATIONS FOR *PLATANTHERA FLAVA* AND *TRIPHORA TRIANTHOPHORA* AND OTHER OBSERVATIONS

PHILIP E. KEENAN

ABSTRACT

New stations for *Platanthera flava* (L.) Lindl. and *Triphora trianthophora* (Sw.) Rydb. were discovered through field studies in New Hampshire and Maine. A short discussion of habits and ecology is also included.

Key Words: *Platanthera flava, Triphora trianthophora,* ecology, New Hampshire

PLATANTHERA FLAVA

Platanthera flava (L.) Lindl., the well-named tubercled orchid, is one of our more infrequently seen orchids. Many botanists and amateur orchid lovers have never seen it. Brackley (1984) considered it uncommon in New Hampshire, listing it for three widely divergent counties: Coos, Cheshire and Strafford. Eastman et al. (1981) listed only one or two records for Maine in the last few decades, while Crow et al. (1981) considered it rare in all of New England with the exception of Connecticut. Once under review for Federal listing, the Government dropped it from further consideration as being more abundant than warranted for listing (Federal Register, 15 December 1980, vol. 45 no. 242).

In the past few years it has been my good fortune to discover three new stations in York County, Maine, three in Rockingham County, N.H. and three in Strafford County, N.H. The most recent discovery in the town of Madbury, N.H. contained more than two thousand plants, many of them bunched together, most of them in bloom, and all within an area approximately fifteen by thirty meters. According to Brackley (personal communication) this is the largest station in New Hampshire. The plants were very robust, a few exceeding the usual heights given—50 cm by Luer (1975) and 7 dm by Fernald (1950)—by several millimeters. The plants are growing in a wet meadow environment, surrounded by forest, and maintained as a meadow by periodic, but not annual, mowing. While scattered in other parts of the meadow, the main site featured a rank growth of sensitive fern (*Onoclea sensibilis*) which grew along the border of the woods and provided a uniform backdrop for the orchids. One could conjecture as to the long-term effect of this invasive weedy fern on the orchid niche. Typical companion plants included *Iris versicolor* (blue flag), *Lilium canadense* (meadow lily), *Lysimachia terrestris* (swamp candles), *Geum rivale* (water avens), *Thalictrum polygamum* (tall meadow-rue), *Spiraea latifolia* (meadowsweet) *Spiraea tomentosa* (steeplebush), *Geranium maculatum* (wild geranium), and *Eupatorium maculatum* (Joe-Pye-weed) among others. An interesting side-light involves the Joe-Pye-weed here: long after all the other Joe-Pye-weed has reached peak bloom and gone beyond, the patch growing beside the tubercled orchid is just beginning to bud, and in some years fails to open because of frost arrival. I have never seen this phenomenon anywhere else.

One of the peculiar characteristics of *Platanthera flava* is the persistence of its flowers. The yellowish-green flower is in prime condition for only about two weeks, but the calyx remains green in many specimens well into September, sometimes until the first frost kills it. After the first two weeks of peak color, the corolla begins to blacken rapidly; the spur, lateral petals and lip become black about the same time. The ovary, however, retains its green color. This differential aging facilitates the off-season chance of identifying the species all summer long. Many of the stems persist through the winter (as does *Goodyera pubescens*).

Unfortunately, many orchid stations (including other orchids of grassy habitats) are at least temporarily obliterated when the landowner mows the meadow at the "wrong" time. Mowing undoubtedly accounts for some of the difficulty in finding this inconspicuous orchid and makes it a little more uncommon.

Color photographs slides, prints and enlargements are in my collection, including the closeup of one specimen with a handsome deep yellow crab spider with two maroon thorax marks on a spike of 40–50 flowers. I have seen many of the white crab spiders with the pink thorax marks but never the yellow. In addition to the photographic documentation, vouchers have been deposited in NHA.

TRIPHORA TRIANTHOPHORA

Triphora trianthophora (Sw.) Rydb., the nodding pogonia or three-birds orchid, is a most fascinating plant which I have been studying for a number of years. During this time I have also discovered three new stations in Holderness, N.H. (Grafton County). This orchid is saprophytic, subterranean and erratic in nature. It is also tiny, pretty and ephemeral. Each flower blooms only for a day—in prime condition; some flowers will remain unfresh into the second day. Usually only one or two flowers open at once, sometimes three. Since there are only one to six buds produced on each plant, the effective bloom period for an individual plant is only about three days. Each one of these three blooming days is usually separated by an interval of several days. The flowering period, therefore, can be as long as two or three weeks, but with only three days of actual open flowers, due to the simultaneous mass flowering of a population on each of these approximately three days. This situation is unique among our wild flowers, and explains why no flowers are detected on several field trips during the anticipated blooming period. In 1974, I made five trips to a *Triphora* station in ten days' time and found it in bloom, in mass, only on the last day. The day of bloom occurred forty-eight hours after a colder than usual night, a phenomenon known as thermoperiodicity. This response has been shown experimentally under artificial conditions also (Luer, 1975). Sometimes an isolated plant in a population will bloom alone, "off schedule" or be a second-day flower. The order of opening is also erratic. The top and bottom bud may open together while the middle one remains closed, or sometimes, when the plant has only two buds, the top one will open first.

In 1984 I observed another interesting occurrence. On August 25 the station was in mass bloom. Eight days later the ovaries of all the plants had been nipped off, while more than half of all the plants had been eaten in their entirety. On the previous August 25, after completing a photographic session with an especially highly-colored clump, I noticed a chipmunk come out of his hole beside a decayed tree trunk which was lying on the ground in close proximity to the prized group of *Triphora*. There was no sign of this clump eight days later. The attractiveness of the succulent stems to rodents has been noted for plants under cultivation and no doubt is also a problem in the wild, as I have observed for several years. It must also account for some of the erratic appearances of this beautiful orchid—here today, gone tomorrow.

Vouchers have been deposited in NHA.

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31 HILLCREST DRIVE
DOVER, NH 03820

FOUR RARE EURASIAN ADVENTIVES IN THE FLORA OF WESTERN MASSACHUSETTS

MICHAEL H. GRAYUM AND MARIAN F. ROHMAN

ABSTRACT

Recent collections of four weedy species of angiosperms native to Eurasia are reported from Hampshire County, Massachusetts. *Elsholtzia ciliata* and *Lepidium perfoliatum* are reported for the first time from western Massachusetts. Three collections of *Poa bulbosa* from the Amherst area mark the first records of this species from New England. *Apera* (*Agrostis*) *interrupta* is reported for the firt time from the eastern seaboard of the United States.

Key Words: Labiatae, Cruciferae, Gramineae, Eurasian adventives, new records, Massachusetts

INTRODUCTION

Botanical collecting by the authors in the Pioneer Valley area of Hampshire County, Massachusetts over the past six years has revealed the presence of four rare angiosperm weeds native to Eurasia. Since the distribution of these species is of general relevance to the New England flora, the collections are detailed below. The order is that of Gray's Manual (Fernald, 1950).

Poa bulbosa L.

Fernald (1950) reported *Poa bulbosa* only as far north as Long Island and Yonkers, New York. It can now be added to the New England flora on the basis of three collections, all from the Pioneer Valley area of Hampshire County where it appears to be becoming rather well established.

The first collection of *Poa bulbosa* from New England was apparently that of the late Harry E. Ahles, as a lawn weed on North Maple Street, Hadley: 21 May, 1979, *Ahles 86583* (MASS, NEBC). The species was later collected in a similar situation along North Pleasant Street, Amherst: 20 May, 1981, *Grayum 3080* (MASS). It has recently been discovered in relative abundance on the campus of the University of Massachusetts, Amherst: 3 May, 1984, *Rohman & Grayum 2335* (MASS).

Apera interrupta (L.) Beauv.

This species has generally been treated in North American floras as *Agrostis interrupta* L. Most recent European authors, however, prefer to segregate the oligotypic genus *Apera,* which (though rather disturbingly polythetic) may be distinguished from *Agrostis sensu stricto* on the basis of the following characteristics [key adapted from Hitchcock (1950) and Tutin (1980)]:

Lemma firm at maturity, shortly bearded at the base (in ours), awned from just below the tip; awn straight, usually at least 4 mm long; upper glume 3-veined; palea strongly 2-nerved, about as long as the lemma; rachilla prolonged back of the palea as a naked bristle .... *Apera*

Lemma thin, glabrous basally or variously hairy or bearded, awnless or awned from near or below the middle; awn, if present, straight or geniculate, often less than 3 mm long; upper glume usually 1-veined; palea usually nerveless and shorter than the lemma, or obsolete; rachilla usually not prolonged or, if so, minutely pubescent to pilose .... *Agrostis*

Although *Apera spica-venti* (L.) Beauv. (= *Agrostis spica-venti* L.) is a rather widespread weed in North America, most records of *A. interrupta* are from the Pacific coast. Gleason & Cronquist (1963) reported a collection from the vicinity of St. Louis, Missouri (*see also* Mühlenbach, 1979), and there have been several recent collections from the midwestern United States and adjacent Canada (*see* Solheim & Judziewicz, 1984). The species seems to be spreading rapidly eastward, having been collected in Missisquoi County, Quebec by 1979. The following specimen, from the campus of the University of Massachusetts, Amherst, Hampshire County, is believed to represent the first collection from the eastern seaboard of the United States: 7 June, 1982, *Rohman & Grayum 2030* (MASS, NEBC).

The following herbaria were checked, without success, for eastern specimens of *Apera interrupta* that might have been overlooked: MASS, NEBC, GH, NY, and MO. It was obviously not possible to check all of the hundreds of herbaria in the eastern United States, so it is conceivable that one or more of these may harbor additional specimens of this rare weed.

Apera interrupta may be distinguished from the more common *A. spica-venti* by several characteristics not alluded to in most North American floras. The following key, which also includes a third

Eurasian species not yet reported from North America, has been adapted from Bor (1970) and Tutin (1980):

Panicle branches long, spreading; lemma shortly bearded at the base; anthers 1–2 mm long ..... *A. spica-venti* (L.) Beauv.
Panicle branches short, erect
  Upper glume awned; lemma shortly bearded at the base; anthers 0.3–0.5 mm long .... *A. interrupta* (L.) Beauv.
  Upper glume shortly awned; lemma glabrous at the base; anthers ca. 1.5 mm long .... *A. intermedia* Hackel

Additional features that may aid in identifying *Apera interrupta* are its narrow (1–4 mm broad), more or less involute leaves and generally shorter ligules (2–5 mm, as opposed to 3–12 mm in *A. spica-venti*). In general, any small, annual, *Agrostis*-like grass with a strict inflorescence and conspicuously awned lemmas should be checked against the description of *Apera interrupta,* which is certainly more widespread than records indicate.

The station for *Apera interrupta* reported above was mowed just three days following the collection, and subsequently ravaged by a construction project. No sign of the species has been seen since.

Lepidium perfoliatum L.

Collected on the campus of the University of Massachusetts, Amherst, Hampshire County: 27 April, 1984, *Grayum & Sleeper 3272* (MASS). This record is apparently the first for Hampshire County, and for western Massachusetts in general. According to unpublished recoreds of H. E. Ahles, the most recent New England collection is from Essex County, Massachusetts, in 1954. Prior to that date, *L. perfoliatum* had been collected in Worcester County, Massachusetts, in 1938, but never any further west in New England.

On the University of Massachusetts campus, *Lepidium perfoliatum* grows alongside *Poa bulbosa* at the same site—the south side of the Student Health Center—formerly occupied by *Apera interrupta.* This commonality of habitat suggests that these three adventive species may owe their introduction to an exotic and rather impure source of soil or, more likely, grass seed. The area was indeed reseeded following a recent construction project, but the collection of *Apera* predated these events. *Poa bulbosa,* as has been noted, is also known from two other disparate locales in the Amherst area. It thus seems improbable that the presence of three of the four adventives reported herein is traceable to a single introduction.

Elsholtzia ciliata (Thunb.) Hylander

Although this rare labiate was collected in Chittenden County, Vermont as recently as 1975 (*Ahles 81660*, MASS), it has not been collected in Massachusetts since a 1958 collection from Essex County (according to unpublished data of H. E. Ahles). The westernmost Massachusetts collection is from Worcester County (1952). The following specimen thus represents the first record from Hampshire County, as well as from western Massachusetts in general: along railroad tracks at east side of Arcadia Lake, Belchertown, 13 September, 1978, *Grayum 1533* (MASS). The site is at an elevation of about 315 feet.

ACKNOWLEDGMENT

We express our sincere appreciation to the late Harry E. Ahles, whose enthusiasm and expertise were an inspiration to legions of botany students (ourselves included) at several different universities, and whose meticulous and voluminous data books contributed substantially to the present report.

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M. H. G.
MISSOURI BOTANICAL GARDEN
P.O. BOX 299
ST. LOUIS, MO 63166

M. F. R.
DEPARTMENT OF BOTANY
UNIVERSITY OF MASSACHUSETTS
AMHERST, MA 01003

THE FIRST RECORD OF *POA BULBOSA* L. (POACEAE) FOR VERMONT

PETER F. ZIKA

In the past 20 years, several adventive weeds reported for the first time from the campus of the University of Vermont have become pests in the state. These weeds include *Geum urbanum* L., *Polygonum caespitosum* Blume var. *longisetum* (DeBruyn) Stewart (Zika et al., 1983) and *Puccinellia distans* (L.) Parl. (Seymour, 1967). Therefore it seems useful to note the occurrence of a new adventive. Vermont's first station for *Poa bulbosa* L. came from a weed patch near a dumpster by Cook Science Building on the University of Vermont campus, in Burlington, Chittenden County, on 6 May 1985. The species was recognizable only because a few days of rainy spring weather had delayed the mowing schedule of the ground crew and allowed some inflorescences to form. For five years the writer had walked past this very spot several times a week and not noticed the species.

The specimens collected (*Zika 8974* NEBC, VT) showed no normal spikelets, only viviparous inflorescences, and aggressively spreading bulbous bases connected by short runners. The species may have been introduced as an impurity in lawn seed or hay bales, or by the muddy construction machinery commonly found on campus.

A check of the Pringle Herbarium showed no *Poa bulbosa* specimens from Vermont or any other New England state. The range map in Hitchcock and Chase (1950) indicated no records of this European weed north or east of New York State. Thus *P. bulbosa* is recorded here as new to Vermont, and as a recent northeastern extension of range. Although Seymour (1982) did not include the species in his New England flora, Marian Rohman (pers. comm.) reports four records from two counties in western Massachusetts, where the species was first collected in the mid-1970's by Harry E. Ahles.

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PRINGLE HERBARIUM
BOTANY DEPARTMENT
UNIVERSITY OF VERMONT
BURLINGTON, VT 05405

BOOK REVIEW

A. C. JERMY AND T. G. WALKER. 1985. *Cytotaxonomic Studies of the Ferns of Trinidad.* Bull. Brit. Mus. Nat. Hist. Bot 13: 133–276. (Price £22.00)

During the course of an earlier study on the ferns of Jamaica, which focused on the cytological features of a tropical island fern flora, it was determined that a broader scope was needed to place the evidence within a larger framework. Accordingly, Trinidad was selected for a similar study and the results are now reported here.

The Bulletin consists of three separate papers. The first by A. C. Jermy is a general review of the geology, soils, climate and vegetation of Trinidad, and the last by Jermy and Walker describes nine sterile hybrids and five new species, three of them diploid and two tetraploid. The main portion of the Bulletin consists of the second paper on "The cytology and taxonomic implications" by T. G. Walker. This is a major contribution to fern cytology and especially to the cytology of tropical American ferns. It contains 155 records of taxa and their cytotypes.

Surveys were made of the island ferns during trips from 1963 through 1974. A list of the species and their chromosome numbers and ploidy levels contains many new reports for American ferns, although some species were previously reported, especially from Jamaica, but also from Mexico, Central America, Puerto Rico, and Brazil.

The results are discussed under the treatments of families and genera and previous reports are integrated with the Trinidad findings. Morphological characters are often included in these accounts as well as details of species complexes and hybrids. The studies are especially critical in difficult groups as *Lygodium,* Gleicheniaceae, *Adiantum, Polypodium, Goniopteris, Asplenium,* and *Blechnum.*

Although the author states that (except for *Polypodium sens. lat.*) the classification of Crabbe et al. (Brit. Fern Gaz. 11: 141–162) is followed, there are in fact departures from that system. For example, *Nephrolepis* and *Oleandra* in a subfamily of the Aspleniaceae rather than the Davalliaceae. The treatment of the Cyatheaceae includes *Cnemidaria* under *Cyathea,* rather than a distinct genus, and *Sticherus* is placed under *Gleichenia.*

Much work is devoted to karyotyping, including a lengthy explanation of a new methodology. Nineteen karyograms are illustrated, some of large ones as *Polypodium phyllitidis* with 148 chromosomes. This impressive data is used to distinguish alloploid taxa as *Lygodium venustum* and 4× *Polypodium aureum* from an interpretation as possible autoploids. However, many problems still persist with this method that place constraints on general evolutionary conclusions.

The cytology has valuable implications for the species classification and the recognition of polyploid complexes. The results emphasize the importance of field study followed by rigorous cytological analysis for an understanding of the dynamics of tropical fern floras. Much more needs to be done, for as Walker comments under the genus *Blechnum* ". . . it is clear that as far as the *B. occidentale* complex is concerned only the tip of the iceberg has been so far exposed." The same could be said for *Adiantum* and other genera where cytological knowledge can be expected to provide critical data on problems evident from taxonomic studies.

ROLLA TRYON
ALICE TRYON
HARVARD UNIVERSITY HERBARIA
22 DIVINITY AVE., CAMBRIDGE, MASS. 02138

BOOK REVIEW

EDWARD G. VOSS. 1985. *Michigan Flora, Part II Dicots* (Saururaceae-Cornaceae). xix + 724 pp. Cranbrook Institute of Science, Bulletin 39 and the University of Michigan Herbarium. (Price $12.50)

Part II of the Michigan Flora continues the outstanding coverage of the plants from Michigan growing outside of cultivation. The coverage includes nearly 1000 species in the apetalous and polypetalous families. The parts of the *Michigan Flora* correspond to the divisions of Gleason's *New Britton and Brown Illustrated Flora.* The style is identical to *Part I* published in 1972; each family treatment includes a key to genera and species, descriptions of taxa, references, county dot maps, and representative illustrations. A key to genera has been purposely omitted until *Part III* is published.

This volume, like *Part I,* is a comprehensive study of Michigan plants. The authors consulted the herbaria in Michigan and selected herbaria throughout the United States for localities and measurements. All measurements stated are from Michigan specimens with the exception of rare plants.

The keys are excellent and easy to use. Nomenclature is up-to-date. If nomenclatural problems occur, Voss discusses his treatment decision. Varieties and subspecies are not included in the keys, but are treated in the writeup. Habitat data were compiled from herbarium sheets, Voss's personal field observations, or from original local information.

The format of the book is superior. The print is clear and use is made of various print sizes and types. The maps and illustrations are clear. Not all species are illustrated, but there is at least one representative species included per genus. A glossary and index to botanical and common names are also included.

Part II as well as *Part I,* of the *Michigan Flora* is a must for every botanist, botanical student, conservationist, or person interested in plant identification in Michigan. For those of us outside of Michigan, this is a valuable reference. This volume may be used by anyone in the northeastern portion of the United States and southeastern

Canada. This book is a "must" purchase and is also a great bargain for only $12.50. I highly recommend *Part II* and eagerly await *Part III.*

C. BARRE HELLQUIST
DEPARTMENT OF BIOLOGY
NORTH ADAMS STATE COLLEGE
NORTH ADAMS, MASSACHUSETTS 02147

IN MEMORIAM

FRANK C. SEYMOUR 1896–1985

The Boston Globe for January 20, 1985, carried a notice that Dr. Frank C. Seymour, 89, who joined NEBC in 1915 and who served as President in 1963 and 1964, died in Dartmouth, MA on January 15. Dr. Seymour was a renowned botanist, author and Congregational minister. Many of his plant specimens are in local herbaria, including the Knowlton Herbarium of the University of Massachusetts. He served as Curator of the Pringle Herbarium at UVM, as Assistant Professor at the University of Florida in Gainesville, and as a research assistant at the Missouri Botanical Garden. He wrote a comprehensive "Flora of New England," which has gone into its second printing. Burial was in Granville, MA.

IN MEMORIAM

HENRY K. SVENSON 1897–1986

Dr. Henry K. Svenson, 89, who joined NEBC in 1919, died on March 4. The following tribute appeared in the *Boston Globe* for Friday, March 7, 1986.

Henry K. Svenson, a botanist who coauthored a guide to the flora of Cape Cod, died Tuesday in Cape Cod Hospital in Hyannis after a long illness. He was 89.

Born in Hinnaryd, Sweden, Mr. Svenson moved to Malden in 1898 and worked in his family's musical instrument manufacturing business in Boston.

In 1921, he graduated from Harvard University. After serving in the US Army, he returned to Harvard, receiving his doctorate in botany in 1929.

From 1930 to 1946, he was curator of the Brooklyn Botanical Gardens in New York. He was chief botanist for the Vincent Astor Expedition to the Galapagos Islands during his first year there.

In 1946, he was appointed curator in forestry and botany at the American Museum of Natural History in New York City. Six years later, he joined the US Geological Survey's military branch, and worked on vegetation maps of Europe and North America.

A year after his retirement in 1966, Mr. Svenson moved to Osterville. In 1979, he coauthored "The Flora of Cape Cod" with Robert W. Pyle.

Mr. Svenson was a member of the Cape Cod Museum of Natural History, the Osterville Men's Club, the Explorers Club of America, the New England Botanical Club and the Joselyn Botanical Society.

Vol 88, No. 854, including pages 157–295, was issued April 29, 1986

INSTRUCTIONS TO CONTRIBUTORS TO RHODORA

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Joan Y. Nickerson
Managing Editor, RHODORA
Phippen-LaCroix Herbarium, Dept. of Biology
Tufts University
Medford, Mass. 02155

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Cover Illustration

An original drawing, seemingly the only one surviving and perhaps the only one ever done for publication by Merritt Lyndon Fernald, used in part to illustrate his article on cranberry species which appeared in RHODORA No. 48 (Fernald, M. L. 1902. The variations and distribution of American cranberries. Rhodora 4: 231–237 & Plate 40). The drawing was rescued from a wastebasket by Dr. Bernice Schubert; it now hangs in the office of Dr. Carroll E. Wood at A. The original Plate 40 caption reads as follows: Fig. 1, *Vaccinium Vitis-Idaea;* fig. 2, *V. Vitis-Idaea,* var. *minor;* fig. 3, *V. Oxycoccus;* fig. 4, *V. Oxycoccus* var. *intermedium;* fig. 5, *V. macrocarpon.*

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CAREX OLIGOCARPA (CYPERACEAE), A RARE SEDGE IN CANADA NEWLY DISCOVERED IN QUÉBEC

STUART G. HAY AND DANIEL GAGNON

ABSTRACT

The first authentic record in Québec of *Carex oligocarpa* is reported in the Ottawa Valley. This discovery, in the Eardley Escarpment, represents a significant outlying northerly station for this rare sedge and is only the seventh known location in Canada. Aspects of the site and forest community are described. The phytogeographic importance of the new record is examined in the context of other unique and rare elements of the *Outaouais* flora.

Key Words: *Carex oligocarpa*, rare, new record, phytogeography, Ottawa Valley Québec, Canada

Carex oligocarpa Schk. ex Willd., a rare Canadian sedge, was recently discovered at the Eardley Escarpment of Gatineau Park in the Ottawa Valley, Québec. This constitutes the first authentic Québec record. The new, outlying station represents a significant range extension and is of considerable interest in view of current work on rare and endangered vascular plants in Canada.

Carex oligocarpa and *C. Hitchcockiana* Dewey are the sole members of the section *Oligocarpae* Carey. These two sedges are rich woodland species of the deciduous forest region of eastern North America. They are often rare in peripheral parts of their range and both are at the northern limit of their distribution in southern Ontario or southwestern Québec.

Floras covering northeastern North America, including the most recent by Scoggan (1978), usually signal the presence of *Carex oligocarpa* in southwestern Québec. The revised edition of Flore Laurentienne (Marie-Victorin, 1964) also includes it, as an addendum. Fr. Louis-Alphonse (1956, M.Sc. thesis, Univ. of Montréal) mapped the species from four locations southeast of Montréal, based on a supposed collection from Philipsburg and other relevant collections from Montréal Island, Chambly and Mt. Johnson conserved at CAN, DAO, MT, and QFA. However, Ball & White (1982) and Boivin (unpublished data) discount the species from the province's flora. A thorough herbarium search for The Rare Vascular Plants of Québec (Bouchard et al., 1983), revealed no substantiating specimens. Erroneously identified specimens of remotely similar species in the section *Laxiflorae* or in the closely allied section *Griseae* evidently account for the mistaken references to *C. oligocarpa* prior to this paper. Although somewhat similar to *C. Hitchcockiana, C. oligocarpa* is readily distinguished by its glabrous leaf sheaths and straight-beaked achenes.

Authentic *Carex oligocarpa* was first discovered in the course of an ecological study of the Eardley Escarpment (fault-scarp of the Precambian Shield) in the Ottawa Valley (Gagnon, 1980, M.Sc. thesis, Univ. of Montréal; Gagnon & Bouchard, 1981). A single collection of the sedge was made but the specimen was misidentified as *C. ormostachya* Wieg. and its proper identity was only revealed by a recent revision of the sheet. The species appears to be very rare on the escarpment. The field data (Gagnon, 1980, M.Sc. thesis, Univ. of Montréal, sample stand #69) indicate that *C. oligocarpa* (*sub C. ormostachya*) was recorded as a single clone from a 1 m^2 quadrat within a 50 m × 20 m sampling plot. The site has not been reexamined since the discovery to assess the species frequency more accurately. The label information on the voucher specimen is as follows: Cté. de Gatineau; Parc de la Gatineau, escarpement d'Eardley. Forêt sèche dominée par *Ostrya virginiana, Tilia americana, Carya cordiformis* (alt. 420′, approx. 45°30′N, 75°54′W). 16 juin 1978. *Gagnon & Bergeron S4M-12* (MT)

The new station for this sedge was found in a young stand of maple-hickory forest community type as described by Gagnon and Bouchard (1981). *Ostrya virginiana* (Mill.) K. Koch was the dominant tree species due to past selective logging of the forest. Subdominants were *Tilia americana* L., *Carya cordiformis* (Wang.) K. Koch and *Juglans cinerea* L. The sapling layer was dominated by *Ostrya virginiana, Tilia americana,* and *Carya cordiformis.* Herbaceous species characteristic of these maple-hickory communities such as *Amphicarpa bracteata* (L.) Fern., *Desmodium glutinosum* (Muhl.) Wood, *Oryzopsis racemosa* (J. E. Smith) Richer, *Phryma* *leptostachya* L., *Sanguinaria canadensis* L. and *Solidago caesia* L. were also recorded. The maple-hickory forests of the escarpment are situated in the lower areas of south-facing slopes where they benefit from increased moisture conditions because of seepage as well as from a warmer microclimate (Gagnon & Bouchard, 1981). The site was situated on a steep (40%) south-facing slope at the foot of the escarpment. The soil was a well-drained Orthic Melanic Brunisol developing on colluvial debris of diopsidic gneiss. The maple-hickory communities of the escarpment generally have soils derived from tills low in calcium, but seepage due to topographical position increases soil nutrient levels, including calcium. This is similar to the situation described in southern Minnesota (Wheeler & Ownbey, 1984) where the preferred habitats of *Carex oligocarpa* are steep, hardwood-covered slopes and ravines on calcareous soils. Mackenzie (1931–35) described this sedge as a calciphile or near-calciphile of rich woodlands in calcareous districts. Other rare or uncommon sedges such as *Carex backii* Boott, *C. cephaloidea* Dewey, *C. cepha-*

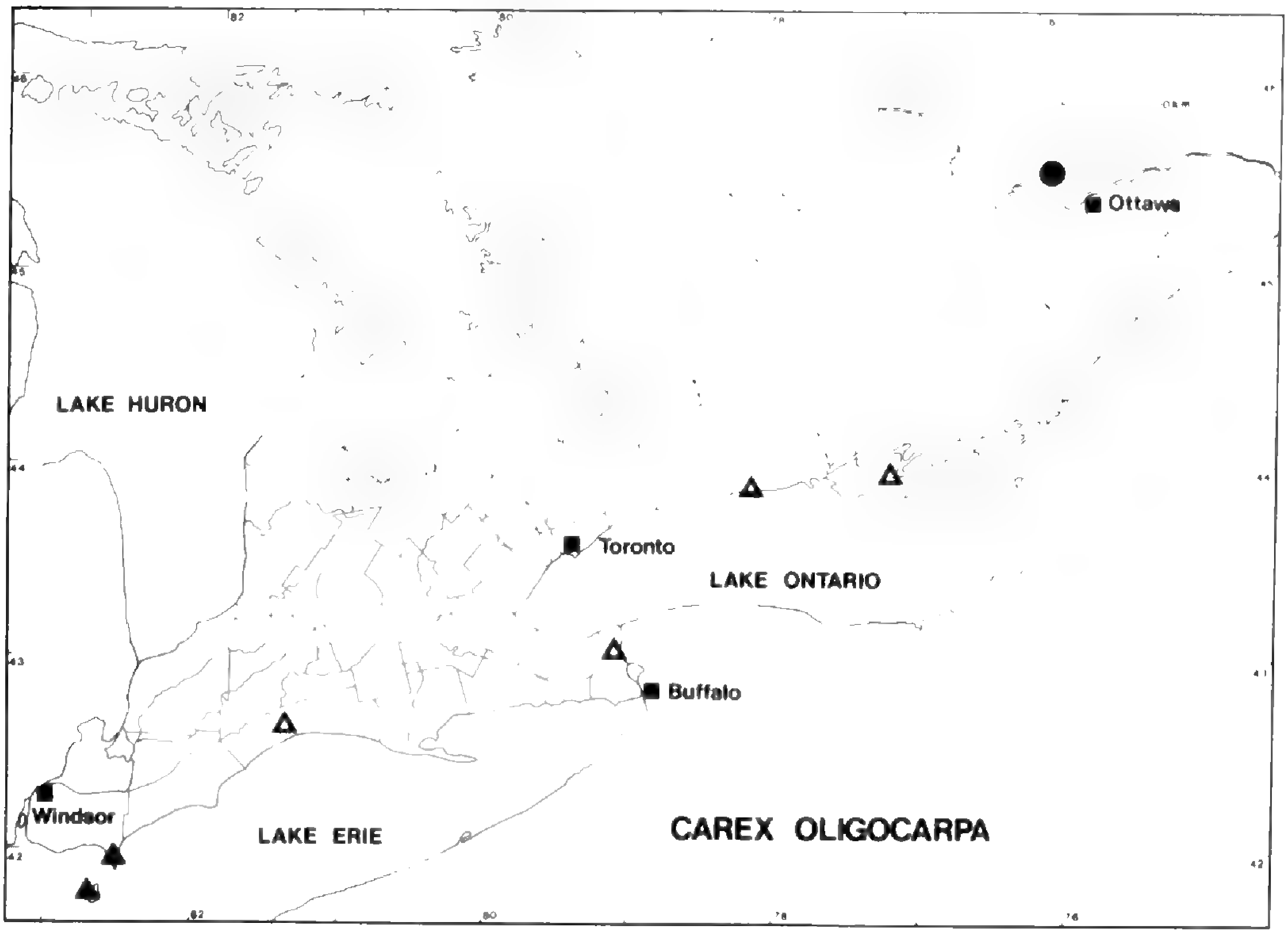

Figure 1. Distribution of *Carex oligocarpa* in southwestern Québec (solid dot, reported in this paper) and southern Ontario (triangles). Open triangles indicate pre-1910 collections; solid triangles represent recent collections at Point Pelee and Pelee Island (map after Ball & White, 1982).

lophora Muhl., *C. Hitchcockiana* Dewey, *C. platyphylla* Carey and *C. sprengelii* Dewey were also recorded in this community and are also usually associated with calcareous woodlands in the northern part of their range.

Carex oligocarpa is essentially a southern and eastern species whose range coincides largely with the eastern deciduous forest. In the Great Lakes region, it reaches its northern limit in southeastern Minnesota, where it has only recently been reported (Wheeler, 1981; Wheeler & Ownbey, 1984), and in southernmost Wisconsin, Michigan and Ontario. Further to the east, it is found in New York State, and isolated populations occur in Vermont, Massachusetts and Connecticut. The species is rare throughout most of its northern range. It is on the lists of rare and endangered vascular plants of Michigan (Wagner et al., 1977), Ontario (Ball & White, 1982), Vermont (Countryman, 1978), Massachusetts (Coddington & Field, 1978) and Connecticut (Dowhan & Craig, 1976; Mehrhoff, 1978).

In Ontario, where its distribution has recently been mapped (Ball & White, 1982), *Carex oligocarpa* is known from only six locations along Lake Erie and Lake Ontario (Figure 1). Four of these records are pre-1910, from Durham Co. (*Macoun s.n.,* DAO #172252), Prince Edward Co. (*Macoun 2031, 31551,* CAN), Elgin Co. (*Macoun 16569,* CAN) and Welland Co. (*Klugh s.n.,* TRT #189605). In 1969, *C. oligocarpa* was discovered in Essex Co. at Point Pelee (*Maycock 13678, in herb. propr.*). The status and habitat of the colonies at Point Pelee National Park have recently been examined by S. Varga (1984). *Carex oligocarpa* has also been discovered in 1981–84 on Pelee Island where A. A. Reznicek and M. J. Oldham have made several noteworthy collections (*Reznicek 6313,* MICH; *Oldham 2571,* CAN, MICH, TRTE; *2664,* CAN, TRTE; *3751,* CAN, MICH, TRTE; *3761,* TRTE; *4284,* TRTE). At the Pelee location, which was too recently reported to be included on the Ontario map by Ball and White (1982), the species appears to be relatively widespread on calcareous soils in deciduous woods and open savannah.

Carex oligocarpa is an important addition to the Québec list of rare vascular plants since in Canada its only other known occurrence is in Ontario, where it is already classed as a rare species. It is the latest addition to an already important contingent of rare vascular plants known from the Eardley Escarpment area of the Ottawa Valley (Brunton & Lafontaine, 1974; Gagnon, 1980, M.Sc. thesis, Univ. of Montréal, 1985; Gagnon & Bouchard, 1981). Bouchard et al. (1983, 1985) have shown that the *Outaouais* region of Québec constitutes the richest floristic sector for rare species in the province. Moreover, a recent study of the ecological distribution of rare species in different plant communities of the central sector of the Ottawa Valley (Gagnon, 1985) shows that the Eardley Escarpment harbors the highest concentration of rare plants, particularly in the oak forests and the maple-hickory communities. The recent addition to the area's flora (Gillett & White, 1978) of such species as *Carex muhlenbergii* Schk. (Gagnon, 1985), *Claytonia virginica* L. (Gagnon, 1980) and now *Carex oligocarpa* is perhaps an indication that still other rare southern elements may be found.

Various authors (Brunton & Lafontaine, 1974; Gagnon, (1980, M.Sc. thesis, Univ. of Montréal); Marie-Victorin, 1934; Raymond, 1950, 1951; Rousseau, 1974) have suggested that post-glacial connections with the Great Lakes may have played a critical role in the establishment of numerous, often rare elements of southern and mid-western affinity in the Ottawa Valley flora. Cody (1982) has examined the distribution of a number of plants in southern Ontario which show disrupted patterns from the extreme southern part of the province to north of Lake Ontario. A number of these species display a fragmented pattern similar to that of *Carex oligocarpa.* They are known from few, scattered populations limited essentially to the Lake Erie–Lake Ontario basins, with outlying colonies occurring northward in the Ottawa Valley. Cody interpreted their distribution in terms of present-day climatic conditions as well as post-glacial migration corridors. He also suggested possible regression from more widespread distributions during the more climatically favorable post-Champlain Sea period.

ACKNOWLEDGMENTS

We are grateful to the curators of CAN, DAO and QFA who made available label information or herbarium specimens originally identified as *Carex oligocarpa* from Québec. B. Boivin (QFA) confirmed our identification and furnished information regarding prior misidentifications of *C. oligocarpa* in Québec. P. W. Ball (TRTE) kindly provided collection data for the Ontario locations and M. J. Oldham (Essex Region Conservation Authority) permitted us to map his recent collections from Pelee Island.

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S. G. H.
HERBIER MARIE-VICTORIN
INSTITUT BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL
4101 EST, RUE SHERBROOKE
MONTRÉAL (QUÉBEC)
CANADA H1X 2B2

D. G.
DÉPARTEMENT DES SCIENCES BIOLOGIQUES
UNIVERSITÉ DU QUÉBEC À MONTRÉAL, C.P. 8888
MONTRÉAL (QUÉBEC)
CANADA H3C 3P8

A NEW SPECIES OF *ILEX* (AQUIFOLIACEAE) FROM HAITI[1]

WALTER S. JUDD

ABSTRACT

A new species, *Ilex blancheana,* is described from a high elevation cloud forest along the Rivìere Blanche, south of Morne la Visite, Massif de la Selle, southern Haiti. This species is distinguished from other tropical American species of *Ilex* by the combination of small, conspicuously veined, and entire margined leaves with obtuse to slightly emarginate apices, and fasciculate inflorescences of three to nine, four-merous flowers, each with an ovoid and very prominent stigma. The hardwood communities of the ravines and the steep, more or less north-facing slopes at higher elevations in the vicinity of Morne La Visite support a diverse and highly endemic flora, which is known mainly through the field work of Erik L. Ekman.

Key Words: *Ilex,* Aquifoliaceae, flora of Haiti

The species described in this paper was discovered in the Massif de la Selle of southern Haiti near Morne la Visite. Field work in this region formed part of an inventory of the flora and fauna of the recently established Morne la Visite National Park. Discovery of this species brings to sixteen the number of species of *Ilex* recorded for Hispaniola (Liogier, 1981). Three other hollies occur in this region of the Massif de la Selle: *Ilex cubana* Loes., *I. fuertesiana* (Loes.) Loes., and *I. macfadyenii* (Walp.) Rehder. In addition *Ilex tuerckheimii* Loes. occurs just to the east in the vicinity of Pic la Selle. A fifth species, *Ilex obcordata* Sw. (= *I. formonica* Loes.), occurs to the west in the high elevation cloud forests of the Massif de la Hotte.

The high elevation cloud forests and pinelands of the Morne la Visite National Park and adjacent areas have been extensively explored by Erik L. Ekman (Ekman, 1926; xerographic copy of unpublished field notes of E. L. Ekman at FLAS), and also were botanized earlier by W. Buch, Padre E. Christ, and Padre L. Picarda (Moscoso, 1943). The diverse and highly endemic flora of the region is in need of additional botanical exploration, however, as evidenced by the discovery of the species described herein.

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Ilex blancheana W. Judd, *sp. nov.* (Figure 1).

Frutex vel arbor parva ad ca. 4 m alta. Folia elliptica vel obovata, (0.9–) 1.5–2.9 cm longa, (0.7–) 1.1–2 cm lata, coriacea, glabra, ad apicem plerumque obtusa, rotundata, vel emarginata, ad basin cuneata; margo integer, planiusculus vel subrevolutus; nervatura brochidodroma; petioli 4–6 mm longi. Inflorescentiae axillares, fasciculatae, cum 3 ad 9 floribus. Flores 4-meri. Pedicelli 3.5–6.5 mm longi, leviter pubescentes. Calyx lobis 0.5–1 mm longis, 0.7–1 mm latis, abaxialiter pubescentibus. Petala oblonga/ovata, 2–2.3 mm longa, 1–1.5 mm lata, alba, leviter pubescentia. Staminodia ca. 1.5–1.7 mm longa. Ovarium globosum, glabrum; stigma conspicuum et ovoideum. Fructus non visus.

Evergreen shrub or small tree to ca. 4 mm tall with smooth bark. Indumentum of unicellular nonglandular hairs to 0.1 mm long. Twigs ridged, sparsely pubescent. Buds triangular, ca. 0.7–1.5 mm long, with two external pubescent scales. Leaves alternate with minute (ca. 0.5–0.7 mm long) triangular stipules; petiole 4–6 mm long, adaxially grooved, slightly pubescent, especially on adaxial surface; blade elliptic to slightly obovate, (0.9–) 1.5–2.9 cm long, (0.7–) 1.1–2 cm wide, flat, coriaceous, the apex obtuse to slightly retuse, rarely acute, with a short blunt mucro, the base cuneate to broadly so, the margin entire, plane to slightly revolute along proximal portion of blade, the adaxial surface lustrous and glabrous, slightly pubescent on impressed midvein, the abaxial surface glabrous, but very sparsely pubescent on extreme proximal portion of midvein, the venation brochidodromous, adaxially obscure, abaxially conspicuous. Inflorescences axillary fascicles, the axis 1–2 mm long, glabrous to sparsely pubescent, bearing 3 to 9 flowers. Flowers imperfect (plants dioecious), 4-merous, each subtended by a pubescent triangular bract to 1 mm long, and paired minute stipules. Pedicels 3.5–6.5 mm long, very sparsely pubescent; bracteoles 2, alternate to opposite, triangular, 0.2–0.4 mm long, pubescent, borne from midpoint to within lower 1/3 of pedicel. Sepals 4, triangular with acute to obtuse apices, 0.5–1 mm long, 0.7–1 mm wide, slightly connate at base, adaxial surface sparsely to moderately pubescent, especially near apex. Petals 4, oblong/ovate with rounded apex, slighlty connate at base, 2–2.3 mm long, 1–1.5 mm wide, white, adaxially slightly papillose/pubescent, abaxially sparsely pubescent. Fertile stamens not seen; staminodia of carpellate flowers 4, filament ca. 1 mm long,

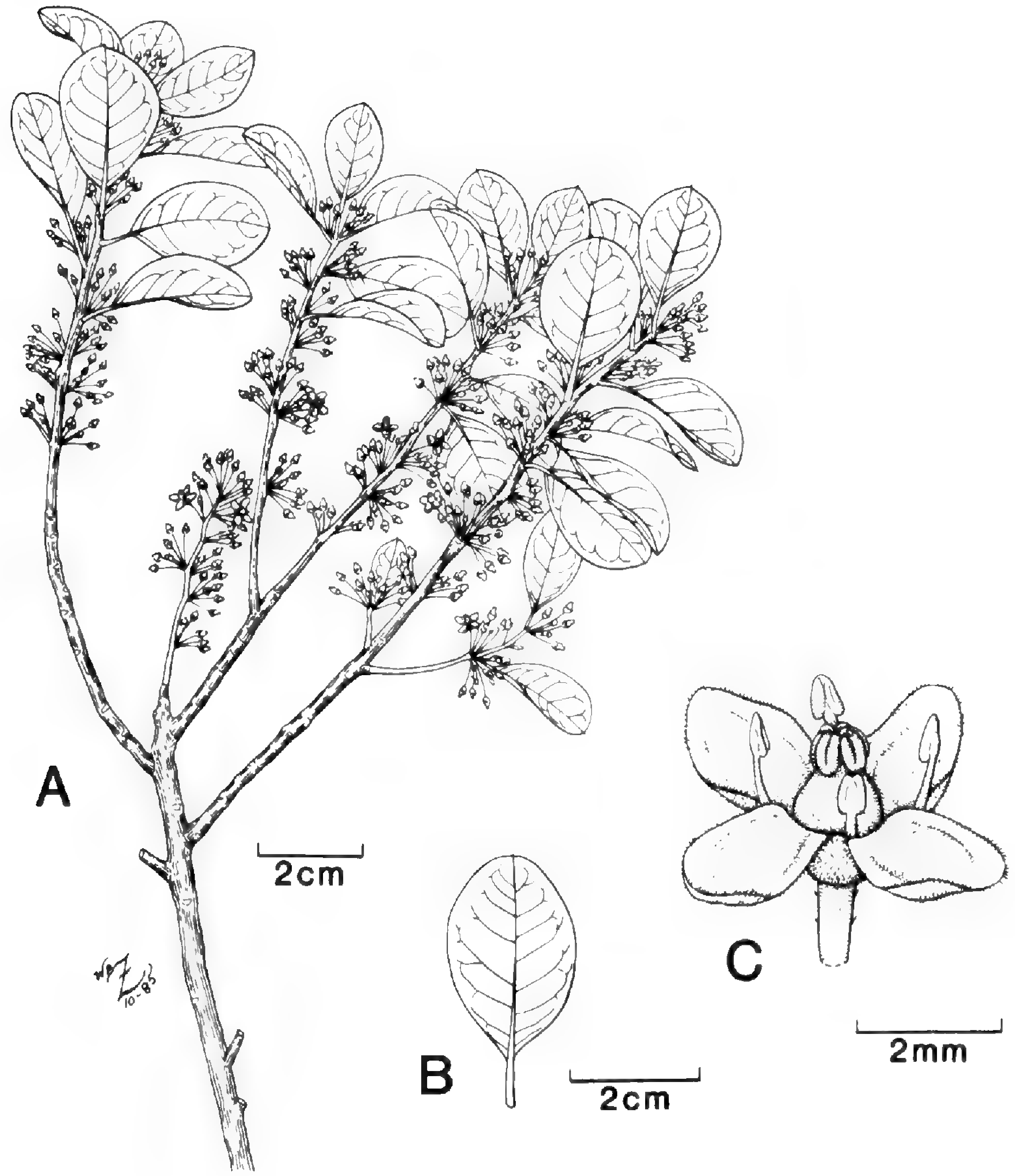

Figure 1. *Ilex blancheana:* A, habit; B, leaf; C, flower. Drawn from the holotype.

slightly adnate to corolla, anther 0.5–0.7 mm long. Ovary 4-loculed, globose, glabrous, terminated by a conspicuous, ovoid, slightly 4-lobed stigma. Drupes not seen.

TYPE: HAITI. Department du L'Ouest: Massif de la Selle, Morne la Visite National Park, cloud forest on upper slope of ravine of Rivìere Blanche near large waterfall, ca. 2.5 km southwest of "Park Center", south of Morne la Visite, ca. 1750–1800 m alt. Uncommon. *Walter S. Judd 4403* (HOLOTYPE, FLAS!; ISOTYPES, A! EHH!, S!).

ETYMOLOGY: The specific epithet refers to the Rivìere Blanche, a beautiful river flowing through the high plateau of the Massif de la Selle in the Morne la Visite region, which supports a high diversity of angiosperm species along its ravine slopes.

Ilex blancheana is easily distinguished from other tropical American species of *Ilex* by the combination of small (i.e., less than 3 cm long), conspicuously veined, and entire margined leaves with more or less obtuse to slightly emarginate apices, and fasciculate inflorescences of three to nine flowers. In addition the flowers are 4-merous, and the stigma is ovoid and very prominent. The species is perhaps most similar to *I. berteroi* Loes. (incl. var. *buchiana* Loes.), which has larger leaves, fewer-flowered inflorescences, and flowers with a conical stigma. Similarity in stigma form is also evident with *I. fuertesiana.* In Liogier's (1981) key to the hollies of Hispaniola *Ilex blancheana* would key to the vicinity of *I. guianensis* (Aubl.) Kuntze, a species of lower elevations with obovate to oblong leaves ca. 5–13 cm long, and *I. obcordata,* a species with only one-flowered pistillate inflorescences.

The cloud forest (i.e., moist forests of mixed hardwoods) and forests of *Pinus occidentalis* Sw. of higher elevations of the Massif de la Selle are diverse and contain numerous endemics (ca. 34% endemism among the flowering plants of Morne la Visite National Park; Judd, unpublished data). Hardwood communities similar to the one in which *Ilex blancheana* was collected occur along the steep more or less north facing slopes of the Massif de la Selle from Tete Opaque, Belle Fontaine, and Pic Cabaio west to Morne la Visite. This forest extends westward to Morne d'Enfer and eastward toward Pic la Selle, and shows much local geographic variation. These cloud forests also extend into the larger ravines (and sinkholes) in the high elevation pinelands of the Massif de la Selle. The Rivìere Blanche contains the best developed hardwood community of any ravine in the Morne la Visite region. Woody taxa occurring with the newly described holly include: *Ardisia fuertesii* Urb.*[1], *A. picardae* Urb.*, *Brunellia comocladiifolia* H. & B. subsp. *domingensis* Cuatr., *Buddleja domingensis* Urb.*, *Bumelia subintegra* Urb. & Ekm.*, *Bunchosa ekmanii* Urb. & Ekm.*, *Calyptranthes* cf. *pitoniana* Urb. & Ekm.* *Cestrum coelophlebium* O. E. Schultz, *C. monoeurum* Urb. & Ekm.*, *C. violaceum* Urb.*, *Citharexylum*

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[1] Species endemic to Hispaniola are indicated by an asterisk.

caudatum L., *Coccoloba picardae* Urb.*, *Daphnopsis crassifolia* (Poir.) Meissn.*, *Dendropanax arboreus* (L.) Decn. & Planche, *Dendropemon bistriatus* Urb.*, *Dendrophthora cupressoides* (Macf.) Eichl., *Didmyopanax tremulun* Krug & Urb.*, *Eremolepis wrightii* Griseb., *Garrya fadyenii* Hook., *Gesneria* spp., *Malpighia macracantha* Urb. & Ndz.*, *Meliosma impressa* Krug & Urb.*, *Miconia favosa* (Desr.) Naud.*, *M. ferruginea* (Desr.) DC.*, *M. selleana* Urb. & Ekm.*, *Myrsine coriacea* (Sw.) R. Br. ex Roem. & Schult., *Ocotea acarina* C. K. Allen*, *O. wrightii* (Meissn.) Mez, *Oreopanax capitatum* (Jacq.) Dcne. & Planch., *Persea anomala* Britt. & Wils., *Picrasma selleana* Urb.*, *Pinus occidentalis* Sw.*, *Rhytidophyllum* spp., *Solanum crotonoides* Lam., *Trema micrantha* (L.) Blume, and *Weinmannia pinnata* L. There is hope that these interesting cloud forests can be preserved through establishment of the Morne la Visite National Park, although at this time clearing and burning are still occurring in the area.

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DEPARTMENT OF BOTANY
220 BARTRAM HALL EAST
UNIVERSITY OF FLORIDA
GAINESVILLE, FL 32611

ADDITIONS TO THE VASCULAR FLORA OF KENT ISLAND, NEW BRUNSWICK

ALEXANDER L. MCILRAITH[1]

ABSTRACT

Ten previously unrecorded species of vascular plants are listed for Kent Island, New Brunswick.

Key Words: Vascular plants, new records, Kent Island, New Brunswick

Kent Island (45°35′N, 66°46′E) is the largest island of the Three Islands group located approximately nine kilometers south of Grand Manan Island, New Brunswick in the Bay of Fundy. Vegetation patterns on the island were described by McCain (1975) and a list of the vascular plant species was also published (McCain et al., 1973).

Documenting the species composition of a small island permits assessment of changes which may occur over long periods of time. Hodgdon and Pike (1969) indicated that such records may shed light on plant dispersal mechanisms and species turnover in island communities.

During the period from May 7 to August 14, 1984, ten previously unrecorded species were found on Kent Island. I do not know whether they were overlooked previously or represent new immigrants; it is reasonable to suggest that at least some have become established in the 15 years since the last plant survey. All the species have been recorded on nearby Grand Manan Island (Weatherby and Adams, 1945). Some species may no longer be present on Kent Island; for example, I did not observe *Rosa rugosa* or *Larix laricina.* Identifications of eight specimens collected were verified by G. Keleher; these are deposited at WIN. Two species were identified in the field but were not collected because of their apparent rarity. Nomenclature follows Kartesz and Kartesz (1980).

SPECIES LIST

Lycopodium clavatum L. (Lycopodiaceae): Collected on a hummock of *Pleurozium schreberi* under *Picea glauca* near center of the island (WIN-41220).

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[1] This paper is Contribution No. 55 of the Bowdoin Scientific Station.

Lycopodium complanatum L. (Lycopodiaceae): Collected in an old field (South Field) located in center of the island (WIN-41214).

Botrychium matricariifolium (A. Braun ex Doll) A. Braun ex Koch (Ophioglossaceae): Observed at the southeastern edge of South Field, close enough to the sea to be exposed to salt spray and high winds. Roland and Smith (1969) indicated that this species has been recorded in exposed habitats in Nova Scotia.

Rosa nitida Willd. (Rosaceae): Collected on east side of sphagnum bog on west side of the island (WIN-41215).

Lathyrus palustris L. var. *pilosus* (Cham.) Ledeb. (Leguminosae): Collected on edge of rocky east shore near middle of the island (WIN-41225).

Acer spicatum Lam. (Aceraceae): Collected in dense woods at north end of the island (WIN—41219).

Euphrasia randii B. L. Robins. (Scrophulariaceae): Collected at north-east end of South Field (WIN-41216). McCain et al. (1973) previously recorded this species only on nearby Sheep Island.

Sambucus racemosa L. var. *pubens* (Michx.) Koehne (Caprifoliaceae): Collected below a bald eagle nest near east shore in open *Picea glauca* woods at north end of the island (WIN-41224).

Carex stipata Muhl. ex Willd. (Cyperaceae): Collected in bog on west shore of the island (WIN-41218). McCain et al. (1973) previously recorded this species only on nearby Hay Island.

Platanthera lacera (Michx.) G. Don (Orchidaceae). A single individual of this species was observed in bloom north of the gull hills at south end of the island.

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DEPARTMENT OF BOTANY
UNIVERSITY OF MANITOBA
WINNIPEG, CANADA. R3T 2N2

THE POLLINATION BIOLOGY OF *CYPRIPEDIUM ACAULE* (ORCHIDACEAE)

Richard W. Davis[1]

ABSTRACT

The pollination biology of *Cypripedium acaule*, the pink lady's slipper, was studied by hand-pollinating flowers in the field and by examining pollination and fertilization patterns in naturally occurring populations near Amherst, Massachusetts. Fruit formation in *C. acaule* appears to be limited by pollinators rather than by other resources. Pollination intensity appears to be independent of floral density.

Key Words: *Cypripedium acaule*, orchid, pollination, Western Massachusetts

INTRODUCTION

The stemless pink lady's slipper, *Cypripedium acaule* Ait., typically grows in acidic soil under a fairly open canopy. The plant consists of two large, oval, basal leaves growing from a rhizome. The solitary flower is borne on a scape arising between the basal leaves, and is subtended by a large, leaf-like bract.

Many observers have noted that *Cypripedium acaule*, even in dense populations, rarely forms capsules (Correll, 1950; Case, 1964; Kurfess, 1965). Brackley (1985) states that fruit set in New Hampshire is consistently low, usually less than 10%. Fruit set may be affected by a lack of pollinators, or by accidents occurring between pollination and fruit maturation (Correll, 1950). Late frosts could also lower fruit set (Case, 1964), as could a lack of food resources. However, the causes of low fruit set have not been studied. The purpose of this paper is to determine why fruits infrequently occur.

The nature of pollination in *Cypripedium acaule* promotes outcrossing (Darwin, 1877). The pollinator enters the flower through a slit in the labellum, but is unable to exit through this slit because of its infolded margins. The pollinator exits by first passing underneath the stigma and then one of the two lateral anthers. Each anther contains a sticky mass of pollen, which is attached to the thorax of the pollinator as a unit by pressure the pollinator exerts against the anther. Absence of a pollen mass is a reliable indicator of a visit by a pollinator to a flower (Plowright et al., 1980).

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[1] Present address: 145 Winsor Avenue, Watertown, MA 02172

After the pollinator crawls beneath and past the anther it passes through a small opening at the base of the flower and flies away. Effective pollinators are too large to enter the flower through this opening, and thus a visit to a flower is a one-way trip. The pollinator may then visit and cross-pollinate a second flower.

The pollinators of *Cypripedium acaule* are bumblebee queens (genera *Bombus* and *Psithyrus*). Although there seem to be no reports of pollinator visits to *C. acaule,* two *Bombus* species have been identified as pollinators. Stoutamire (1967) identified *Bombus vagans* and *B. borealis* queens as probable pollinators, and Plowright et al. (1980) found several *B. vagans* queens carrying pollen masses.

Bumblebees are probably attracted to the lady's slipper flower by its color and by a sweet, sugary smell concentrated in the sepals and lateral petals (Stoutamire, 1967). There do not seem to be any rewards for pollinators. Nectar is not secreted, and bumblebees are unable to collect the pollen because of the anther's position on the flower (R. Davis, personal observation).

The lack of pollinator rewards in a bumblebee-pollinated flower is of importance in understanding its pollination biology. Bumblebees have been shown to avoid flowers lacking rewards after sampling them, in favor of flowers which do offer rewards (Heinrich, 1979). This obviously adaptive behavior on the part of bumblebees should lead to lower fruit set in deceptive, non-rewarding flowers. This condition has been shown to be true for other orchid species not offering food rewards, such as *Calopogon tuberosus* and *Calypso bulbosa* (Ackerman, 1981; Boyden, 1982; Thien and Marcks, 1972). However, lower fruit set in orchids is offset by the greater number of seeds produced in a single capsule, which in *Cypripedium acaule* ranges from 14,000 to 54,000 seeds per capsule (Withner, 1959).

It is hypothesized that the formation of large flowering populations might enhance the reproductive success of *Cypripedium acaule;* there might be a positive correlation between floral density and attractiveness to pollinators, with more pollinators visiting the denser populations. The denser populations, by massing both visual and olfactory cues, could be more successful at attracting inexperienced bumblebees, and increase the number of pollinated flowers within a population.

METHODS

On a site near Mt. Holyoke, in Hadley, Hampshire County, Massachusetts, an unpollinated population of 85 flowers was selected for experimental hand-pollination with cross- and self-pollen. On 2 June 1983, 75 flowers were cross-pollinated with the pollen obtained from neighboring flowers, which appeared to be separate individuals; single pollen masses were removed with a finger tip and applied to each stigma. The ten remaining flowers were pollinated with self-pollen. In April 1984, the number of mature capsules from 1983 was counted; mature capsules successfully overwinter and may persist for at least two years because of the lignification of both the scape and capsule wall.

Three belt transects were established at this same site in 1983 to observe pollination and fertilization patterns in natural populations. Each transect was ten meters wide, beginning and ending at the borders of each subpopulation. Two of the transects were twenty meters long, the third ten meters long. In 1984 these same three transects were used again, along with six new transects at Mt. Holyoke. Six transects were also established at Rattlesnake Gutter Road in Leverett, Massachusetts, and three at Teewaddle Hill Road, also in Leverett, for a total of 18 transects. These transects ranged from 5 to 22 meters in length.

The number of flowers was counted in each belt transect. Each flower was inspected for removal of pollen masses; pollen masses were judged removed if the anther was empty. Evidence of pollination such as pollen on the stigma or an enlarged ovary and collapsed labellum was also recorded.

The number of pollen masses removed was counted in 1983 on 9–10 June, when the flowers were rapidly senescing. In 1984 the counts were made on 9–11 June. In 1983 the number of pollinated flowers was recorded on 22 June, after all of the flowers had senesced. In 1984 pollinated flowers were recorded simultaneously with the counting of the removed pollen masses. Pollinators landing on or entering flowers were also recorded.

RESULTS

Cypripedium acaule appears to be highly fertile. Out of 75 cross-pollinated flowers, 56 (75%) set fruit. Seven of the 10 self-pollinated flowers (70%) also formed capsules. These results are similar to those obtained by Newhouse (M.S. thesis, Michigan State, 1976), in which she had 100% fruit set with 4 cross-pollinated flowers and 2 selfed flowers. Newhouse enclosed 8 unpollinated flowers, none of which formed capsules; autogamy does not seem to occur in the absence of pollinators.

The results (Table 1) suggest that *Cypripedium acaule* is infrequently visited by pollinators. Out of a total of 278 flowers in 1983, only 13.3% of the pollen masses were removed, and 9.4% of the flowers pollinated. In 1984, out of 986 flowers, 6.5% of the pollen masses were removed and 4.3% of the flowers pollinated. Other observations supporting infrequent pollinator visits to *C. acaule* come from Plowright et al. (1980), who found that only 3%–6% of the pollen masses were removed from two populations in New Brunswick.

Table 1. Summary of Field Observations, 9–10 June 1983 and 9–11 June 1984. (1983 transects = 3; 1984 transects = 18.)

Data Category	1983	$\bar{X}$	SD	Range	1984	$\bar{X}$	SD	Range
Flowers	278	92.7	69.7	26–165	986	54.8	42.1	12–162
Pollen Masses Removed	74	24.7	11.0	14–36	128	7.1	7.9	0–34
Pollinated Flowers	26	8.7	4.9	3–12	42	2.3	2.6	0–11

Several pollinator visits and pollinators were observed in 1983 and 1984. On 10 June 1983 two pollinators were seen at Mt. Holyoke, both of them bumblebee queens. One was observed entering a flower and exiting with a pollen mass on her thorax. The other, a *Psithyrus ashtoni* queen, a species not previously known to visit *Cypripedium acaule,* was found inside a flower with a pollen mass on her thorax.

Nine bumblebee queens were seen landing on or entering flowers on 2 June 1984, all of them at the same site near Mt. Holyoke. Five entrances and exits by bumblebees were observed. Two of these bees carried pollen masses into flowers, and deposited them on the stigmas of the visited flowers.

Pollination in *Cypripedium acaule* seems to be density-independent. No significant relationships were found between *C. acaule* flower density and either the percentages of pollen masses removed or the percentages of pollinated flowers, using the Spearman Rank Correlation Test ($R_S = -0.1560$ and -0.3476, repectively; $N = 18$).

DISCUSSION

In light of the relatively high fertility of *Cypripedium acaule,* and the low frequency of pollen mass removal, capsule formation is overwhelmingly pollinator-limited. *C. acaule* thus follows the same pattern as other deceptive, non-rewarding orchids, which set relatively few fruits but offset this limitation by producing a large number of seeds within a mature fruit.

Because bumblebees quickly learn to avoid non-rewarding flowers, it is not surprising, in retrospect, that pollination intensity and floral density should be randomly associated. When low densities of flowers are as effective as greater densities in attracting pollinators, what may be of more importance is the density of pollinators in the foraging range of *Cypripedium acaule.* If *C. acaule* flowers are typically pollinated by "naive" bumblebees unfamiliar with *C. acaule,* the number of pollinator visits will depend upon the number of naive bees in the vicinity; these bees may visit the same number of flowers in a given area irrespective of floral density.

Othe plants co-flowering in association with *Cypripedium acaule* could also affect *C. acaule* fruit set if they attract bumblebees into the area. Co-flowering plants located in the belt transects included *Maianthemum canadense, Trientalis borealis, Gaylussacia baccata, Vaccinium angustifolium* and *V. stamineum.* The most wide-spread associate was *M. canadense,* which was located in all transects, sometimes in great density. However, *M. canadense* is pollinated by solitary bees and Dipterans (Thaler and Plowright, 1980). One bumblebee, a worker, was seen foraging on an *M. canadense* inflorescence on 2 June 1984, but this bee was too small to have been an effective pollinator of *C. acaule.* There was some casual evidence, however, that a positive relationship might exist between the presence of the ericaceous shrubs, which are bumblebee-pollinated, and an increased number of pollinator visits to the associated *C. acaule* populations; this possible association might be worth further study.

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DEPARTMENT OF BOTANY
UNIV. OF MASS.
AMHERST, MA 01003

RE-EVALUATION AND LECTOTYPIFICATION OF *SCIRPUS RETROFRACTUS* L.

RICHARD CARTER[1] AND CHARLES E. JARVIS

ABSTRACT

The nomenclatural history of *Cyperus retrofractus* (L.) Torr. is discussed. An authentic Linnaean specimen is reinterpreted as the lectotype for the basionym *Scirpus retrofractus* L. and arguments are made for the reapplication of this name to a species which, since 1906, has been called *Cyperus dipsaciformis* Fernald.

Key Words: Cyperaceae, *Cyperus retrofractus, C. dipsaciformis, C. hystricinus, C. plukenetii,* nomenclature, typification

The *Cyperus retrofractus* complex consists of three North American species for which there are four names available. These species are widely distributed in xeric habitats throughout much of southeastern United States. Kükenthal (1936) in his comprehensive treatment of *Cyperus* placed this complex in section *Umbellati* which is composed of perennials with umbellate inflorescences of simple spikes and few-flowered subterete spikelets. Members of the *Cyperus retrofractus* complex are distinguished from other *Umbellati* by their uniformly retroflexed spikelets and relatively larger akenes and spikelet scales. This group has had a turbulent nomenclatural history (summarized in Table 1) that began with Linnaeus' description of *Scirpus retrofractus* in *Species Plantarum* (1753) p. 50:

> *retrofractus.* 17. SCIRPUS culmo triquetro,umbella ſimplici:ſpicarum floſculis retrofractis.
> Cyperi genus indianum, panicula ſpecioſa, ſpiculis propendentibus atris. *Pluk. phyt.* 415. *f.* 4.
> *Habitat in* Virginia. ♃

In 1805 (p. 375) Martin Vahl treated *Scirpus retrofractus* under *Mariscus* with *Scirpus retrofractus* L. as a synonym. This treatment was followed by Elliott in 1821 and again by Torrey in 1836. However, Torrey (*in* Gray, 1848) later transferred the species to *Cyperus,* thus making the currently accepted combination *Cyperus retrofractus* (L.) Torr. There were apparently few problems in applying this

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[1] Present address and that to which reprint requests should be sent: Department of Biology, Valdosta State College, Valdosta, Ga 31698

name until 1906, when Fernald segregated and described two additional species, thus making it necessary to determine exactly what Linnaeus meant by *Scirpus retrofractus*. The original diagnosis is brief and on its own is of little help. As was usual for his time, Linnaeus cited no specimens but did cite an illustration by Leonard Plukenet (tab. 415, fig. 4: 1742) in the synonymy of the species. Fernald (1906) used this illustration as his basis for application of the name *C. retrofractus* (L.) Torr. This interpretation was followed by Small (1933), by Kükenthal in 1936 (although he treated the species as varieties), and by Horvat (1941). In the meantime, however, Fernald learned that the Linnaean Herbarium (LINN) possessed a specimen labeled by Linnaeus "17 retrofractus" (no. 71.36; *see* Savage, 1945). From a photograph of the specimen, Fernald could tell it was not the same plant depicted by Plukenet but was instead, he thought, the related glabrous species he had described in 1906 as *C. hystricinus*. This left Plukenet's plant, which had been called *C. retrofractus*, without a name; so Fernald in 1945 rearranged his 1906 nomenclature and reduced *C. hystricinus* to a synonym of the newly interpreted *C. retrofractus* (L.) Torr. and described the plant illustrated by Plukenet as *C. plukenetii*. In doing so, Fernald named and described all three species in the complex.

Recently, the Linnaean specimen has been re-examined by us and determined to be neither the glabrous species that Fernald (1945) thought it was (previously described as *Cyperus hystricinus* in 1906) nor the plant in Plukenet's illustration cited by Linnaeus (1753). Instead, it is what since 1906 has been called *C. dipsaciformis* Fernald, and a member of the only species in the group to which the name "retrofractus" has not been applied. In light of this unsettling information, arguments can be made for taking either of two courses.

First, one could argue that it would be preferable to adopt the pre-1945 view of Fernald and others, and accept as the type Plukenet's illustration. This solution has two advantages: (1) since this approach has already been taken and the species have already been treated as varieties in this manner by Kükenthal (1936), it would prove nomenclaturally more conservative if they are treated as varieties again; (2) the plant in Plukenet's figure has been unequivocally attributed by Fernald (1906) to the most morphologically distinctive, central, and most abundant and widespread of the three species. By taking this course, the taxonomy would be in greater concordance with the nomenclature and hence more logical.

The other solution is to accept a Linnaean specimen as the lectotype of *Scirpus retrofractus* L. Clarke (1895) argued convincingly for the use of marked specimens of Cyperaceae at LINN instead of the sometimes vaguely rendered and often confusing illustrations cited by Linnaeus. However, each case must be judged on its merits and the sources of information used in the protologue carefully weighed. Further, Recommendation T4b of the ICBN (Voss, 1983) requires that when there is a choice, a specimen should be selected as lectotype over an illustration. Finally, Article 8.1 states that the author who first designates a lectotype must be followed. Fernald did not designate a type in 1906; he wrongly assumed the plate to be the basis of the name. However, in 1945 Fernald was aware of both elements and clearly referred to the specimen at LINN as "the type."

In addition to the previously cited authentic specimen at LINN, there is at the Linnaean Herbarium in Stockholm (S) a specimen (IDC Microfiche no. 21.1) bearing the number "17" and the annotation "retrofractus." However, these annotations are not in Linnaeus' hand and we therefore do not regard the specimen as a syntype. Moreover, a photograph of this specimen has been examined by us and determined definitely not to be in this complex.

Certain other information in Linnaeus' hand found on the reverse side of specimen 71.36 (LINN) and pertaining to its identity indicates that it was sent to Linnaeus by Gronovius ("Gron.") and is evidently number "457" of John Clayton. It was therefore collected in Virginia (Savage, 1945; Stearn, 1957; Reveal, 1983). It is interesting to note that Linnaeus did not cite this specimen indirectly in the protologue as he did in other instances of Clayton material acquired by Gronovius, presumably because it seems not to have been cited in Gronovius' *Flora Virginica* (1739).

Plukenet's illustration is rather questionably matched by a specimen in his herbarium, now found in the Sloane Herbarium at BM (HS 92: 79). However, if that specimen was the basis of the illustration, significant modifications were made in the form and arrangement of the heads. Linnaeus would not in any case have seen this specimen and he referred Plukenet's polynomial to *Scirpus retrofractus* on the basis of the information available in the illustration.

In light of the information presented here, we believe it best to follow Fernald (1945) in accepting the specimen no. 71.36 (LINN) as the lectotype of *Scirpus retrofractus* L. and to make the necessary nomenclatural adjustments (Table 1); that is, we apply the name

Table 1. Historical application by various authors of names in the *Cyperus retrofractus* complex.

Fernald Names[1]	Pre-1906	Fernald (1906) Horvat (1941)	Kükenthal (1936)	Fernald (1945)	Present Treatment
"plukenetii"	*retrofractus*	*retrofractus*	var. *retrofractus*	*plukenetii*	*plukenetii*
"hystricinus"	"	*hystricinus*	var. *hystricinus*	*retrofractus*	*hystricinus*
"dipsaciformis"	"	*dipsaciformis*	var. *dipsaciformis*	*dipsaciformis*	*retrofractus*

[1] Because Fernald used modern type-methods and his names can be unambiguously applied, they are used here as convenient reference points.

Scirpus retrofractus L. to what has been passing since 1906 as *C. dipsaciformis* Fernald, and relegate *C. dipsaciformis* to the synonomy of *C. retrofractus* (L.) Torr., and re-establish *C. hystricinus* Fernald. Below are currently accepted names with their synonyms:

1. **Cyperus retrofractus** (L.) Torr. in Gray, Man. Bot. North. U.S. 519. 1848.

    Scirpus retrofractus L., Sp. Pl. 1:50. 1753. TYPE: U.S.A. Virginia, *Clayton 457.* (LECTOTYPE: no. 71.36 LINN!).

    Mariscus retrofractus (L.) Vahl, Enum. Pl. 2:37. 1806.

    C. dipsaciformis Fern., Rhodora 8:127. 1906. TYPE: U.S.A. District of Columbia, Washington, 22 July 1896, *Steele s.n.* (HOLOTYPE: GH!; ISOTYPE: US!).

    C. retrofractus (L.) Torr. var. *dipsaciformis* (Fern.) Kükenthal in Engler, Pflanzenreich IV(20)101: 509. 1936.

2. **Cyperus hystricinus** Fern., Rhodora 8: 127. 1906. TYPE: U.S.A. New Jersey, near Haddenfield, 13 October 1867, *C. F. Parker s.n.* (HOLOTYPE: GH!).

    C. retrofractus (L.) Torr. var. *hystricinus* (Fern.) Kükenthal in Engler, Pflanzenreich IV(20)101: 509. 1936.

3. **Cyperus plukenetii** Fern., Rhodora 47:110. 1945. TYPE: U.S.A. Virginia, Princess Anne County, Cape Henry, 28 and 29 July 1934, *M. L. Fernald* and *B. Long* (HOLOTYPE: GH!)

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R. C.
DEPARTMENT OF GENERAL BIOLOGY
VANDERBILT UNIVERSITY
NASHVILLE, TN 37235

C. E. J.
BRITISH MUSEUM (NATURAL HISTORY)
CROMWELL ROAD
LONDON SW7 5BD
UNITED KINGDOM

SYNOPSIS AND ACHENE MORPHOLOGY OF *POLYGONUM* SECTION *POLYGONUM* (POLYGONACEAE) IN CANADA

Steven J. Wolf[1] and John McNeill

ABSTRACT

Thirteen species and two subspecies are recognized in *Polygonum* section *Polygonum* in Canada. Four achene types are recognized in the section: smooth, roughened, papillose and striate-papillose. Descriptions, a discussion of comparative features, distributions, chromosome numbers and a key to the species are presented. Two new taxa are described: *P. caurianum* ssp. *hudsonianum* and *P. franktonii*.

Key Words: *Polygonum* section *Polygonum*, Polygonaceae, synopsis, achene morphology, Canada

In Canada, *Polygonum* section *Polygonum* comprises an extremely variable assemblage of both native and introduced taxa which occur in a variety of habitats from coastal shores, beaches and saline marshes to dry, disturbed, weedy habitats along roadsides, footpaths and wasteplaces. The section is characterized by its flowers borne in axillary clusters, its jointed petioles and a basic chromosome number of $x = 10$. Existing treatments of the section in Canada are extremely divergent in the number of species that they include and in criteria used for species delimitation. Fernald (1950) recognized 12 Canadian species in *Polygonum* section *Polygonum*, one of which, *P. douglasii* Greene, is no longer inlcuded in the section (Löve and Löve, 1956; Mertens and Raven, 1965). In addition, Fernald (1950) noted that the name *P. aviculare* L. encompassed a vast array of forms, and recognized three varieties in this taxon. Gleason (1952) recognized six species in the section in eastern Canada and treated the *P. aviculare* complex as a single polymorphic species. In an account of chromosome numbers, Löve and Löve (1956) recognized 21 species and a number of infraspecific taxa in eastern Canada, and attempted to clarify the application of the name *P. aviculare*.

In more recent treatments of *Polygonum* section *Polygonum*, particular attention has been focused on defining the limits of the *P.*

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[1] Present address: Department of Environmental, Population and Organismic Biology, University of Colorado, Boulder, Colorado 80309.

aviculare complex and establishing taxonomic criteria for the delimitation of its segregates (Styles, 1962; Mertens and Raven, 1965; Savage and Mertens, 1968; Jones and Mertens, 1970; McNeill, 1981). Styles (1962) recognized four species in the *P. aviculare* complex in the British Isles and established the utility of such characters as heterophylly, fruit size and shape, perianth features and chromosome number in distinguishing members of the section. Styles (1962) concluded that *P. aviculare s. str.* is a heterophyllous hexaploid while *P. arenastrum* Boreau is a homophyllous tetraploid. Mertens and Raven (1965) extended Styles' (1962) work to North America and recognized nine species, which included seven in Canada and three in the *P. aviculare* complex: *P. aviculare s. str., P. arenastrum,* and *P. boreale* (Lange) Small. Shortly thereafter, Savage and Mertens (1968) recognized a fourth species in the *P. aviculare* complex, *P. buxiforme* Small. Scoggan (1978) recognized eight species in *Polygonum* section *Polygonum,* suggested that *P. aviculare s. str.* is very rare in Canada, and included a large number of synonyms under *P. arenastrum.* Recently, McNeill (1981) demonstrated that both the homophyllous tetraploid *P. arenastrum* and the heterophyllous hexaploid *P. aviculare* are very common in eastern Canada and are readily distinguishable by a number of additional features. These features include achene size and shape, length of perianth segments, pollen type, and leaf size and shape.

In the course of McNeill's (1981) investigation of the *Polygonum aviculare* complex, it became apparent that it is comprised of a number of both native and introduced taxa, some of which have never received formal taxonomic recognition. It also soon became apparent that the entire section *Polygonum* in Canada needed to be re-examined with respect to the taxonomic criteria employed in the group, especially in light of more recent cytological data (Moore, Mertens and Highwood, 1970; Wolf and McNeill, 1986). The investigation reported here was undertaken in an effort to delimit the taxa of *Polygonum* section *Polygonum* in Canada and to re-evaluate taxonomic criteria, particularly achene features, that have been traditionally employed in the group. This study is based on more than 200 field collections as well as specimens from the following herbaria: ACAD, ALTA, BSUH, C, CAN, CU, DAO, GH, MO, NYS, QUC, TRT, US, VT, WAT and WIN.

MORPHOLOGY AND TAXONOMIC CRITERIA

Although many species of *Polygonum* section *Polygonum* appear superficially similar, they are readily distinguished by a combination of features of the general habit, leaves, ochreae, fruiting perianth, and achenes. The following discussions detail morphological variation and characters of taxonomic significance within the section.

HABIT. All species of the section are herbaceous annuals. Habit varies from dense, prostrate mats to loosely ascending or erect. Most species are glabrous; however, *Polygonum buxiforme* is frequently gray-glaucescent and *P. raii* Bab. is glaucous. Stem height varies from 2 cm in *P. caurianum* Robins. ssp. *caurianum* up to 2 m in *P. ramosissimum* Michx., with such species as *P. buxiforme* and *P. ramosissimum* having somewhat woody and thickened bases. Other diagnostic features include elongated internodes as in *P. neglectum* Besser and *P. erectum* L., branching from the base in *P. caurianum* and *P. raii,* and upcurved branching in *P. achoreum* and *P. prolificum* (Small) Robins.

LEAVES. Several features of the leaves are diagnostic for the various species. These include leaf length, shape, apex, and petiole length. Leaf shape varies from linear (*P. neglectum*) to oblong or obovate in several species and apices vary from acuminate to acute, obtuse or rounded. Leaf length varies from 3 mm in *P. caurianum* ssp. *caurianum* up to 60 mm in *P. erectum* and *P. ramossissimum.* Also characteristic of some species is a condition, termed heterophylly, in which leaves of two markedly different sizes occur on the same plant. In the heterophyllous *P. aviculare, P. erectum* and *P. ramosissimum* cauline leaves are more than three times as long as leaves on the lateral branches.

OCHREAE. Ochrea length in *Polygonum* section *Polygonum* varies from 1–10 mm with most ochreae becoming brown and lacerate with age. However, in such species as *P. buxiforme* and *P. erectum* they remain hyaline-silvery and intact, and are therefore usually quite conspicuous and diagnostic for these two species. Ochrea venation is diagnostic for some species, particularly *P. raii* with 3–5 nerves. It is sometimes confused with the more southerly *P. glaucum* Nutt., which has 8–16 nerves.

FRUITING PERIANTH. Several features of the fruiting perianth are important in the delimitation of the species of *Polygonum* section *Polygonum*. Among these are total length, the degree to which the segments are divided and whether they overlap, the shape of the perianth tips, and color of the margins. Perianth length varies from 1.6 mm in *P. caurianum* ssp. *caurianum* to 5.5 mm in *P. raii*, with the length of the longest segment being important in delimiting the subspecies of *P. caurianum*. The degree to which the perianth segments are divided relative to their total length is very useful in the delimitation of species. In *P. achoreum* Blake the perianth is divided one third or less, in *P. arenastrum* it is divided half way and in the other sepcies it is divided two-thirds to three-fourths or more. Also, in such taxa as *P. arenastrum*, *P. neglectum* and *P. caurianum* ssp. *caurianum* the segments do not overlap in fruit, while in the remaining taxa they do overlap. Perianth tips in most species are flat and flared; however, in such species as *P. buxiforme*, *P. erectum* and *P. fowleri* Robins. they are conspicuously cucullate. Perianth margins are mostly white to pink within species, with the exception of yellow-green in *P. achoreum*, *P. erectum* and *P. ramosissimum*, and purple in *P. caurianum* ssp. *caurianum*.

ACHENES. Traditionally, achene characters such as size, color, shape, and surface texture have been heavily relied upon in the delimitation of species in *Polygonum* section *Polygonum;* however, some of these characters have never been satisfactorily described or defined. Additionally, the fact that many species produce elongated, exserted achenes in late season, in addition to normal achenes, has led to a proliferation of names in the section. Achene size is diagnostic for many species, particularly those of the *P. aviculare* complex, and varies from 1.5–2.2 mm in *P. caurianum* ssp. *caurianum* to 3.5–5 mm in *P. raii*. Most species have brown to dark brown achenes, with the exception of *P. achoreum* (yellow-green to tan) and *P. caurianum* ssp. *caurianum* (dark brown to purple). Achene shape in all species is trigonous; however, the relative width and shape of the individual sides are diagnostic for most species. Species such as *P. aviculare* and *P. erectum* have three subequal convex sides; *P. buxiforme* has three convex sides, one of which is broader than the other two; such species as *P. arenastrum* and *P. franktonii* S. J. Wolf & McNeill have one narrow concave side and two broad convex sides. The other species have various combinations of convex and concave sides.

Although achene features have been consistently used in the identification of the taxa of *Polygonum* section *Polygonum*, the descriptive terminology has heretofore been vague, ill-defined and sometimes technically incorrect. Such terms as smooth, glossy, shining, lustrous, sub-lustrous, dull, striate, granular and punctate are most frequently used in keys and descriptions of the species (Fernald, 1950; Löve and Löve, 1956; Styles, 1962; Mertens and Raven, 1965; Savage and Mertens, 1968; Mitchell and Dean, 1978; Scoggan, 1978). We recognize four achene surface types in *Polygonum* section *Polygonum:* smooth, roughened, papillose and striate-papillose. Smooth surfaces, which have no ornamentation, are characteristic of *P. raii* and *P. ramosissimum* (Figures 1A & 1B). In such species as *P. fowleri* and *P. caurianum* the achene surfaces have no ornamentation, but appear roughened (Figures 1C & 1D). The achene surface of *P. achoreum* has previously been described as granular; however, the surface is actually densely papillose (Figures 2A & 2B). The most common achene surface type in the section, striate-papillose, which is characteristic of all species previously included in the *P. aviculare* complex, has never been adequately described. Previously, this surface type has been referred to as dull, striate or punctate. However, it is evident even under relatively low magnification that the surface consists of longitudinal rows of papillae (Figures 2C & 2D).

Many species of *Polygonum* section *Polygonum* produce elongated, exserted fruits in late season in addition to normal fruits, produced throughout the growing season. The late-season fruits, which are 2–3 times as long as normal fruits, are usually olivaceous, lanceolate, smooth surfaced and have a very thin seed coat. In most species fruits occur only late in the growing season, i.e., after late September; however, *P. caurianum* ssp. *hudsonianum* S. J. Wolf & McNeill has a preponderance of them as early as August 1. Failure to distinguish late-season fruits has led to a proliferation of names in the section. For example, *P. exsertum* Small is actually *P. ramosissimum* with late season fruits (Gleason, 1952; Mertens and Raven, 1965). Although late-season fruits cause some difficulty in species identification, normal fruits are also usually present and diagnostic perianth and vegetative features are still also evident.

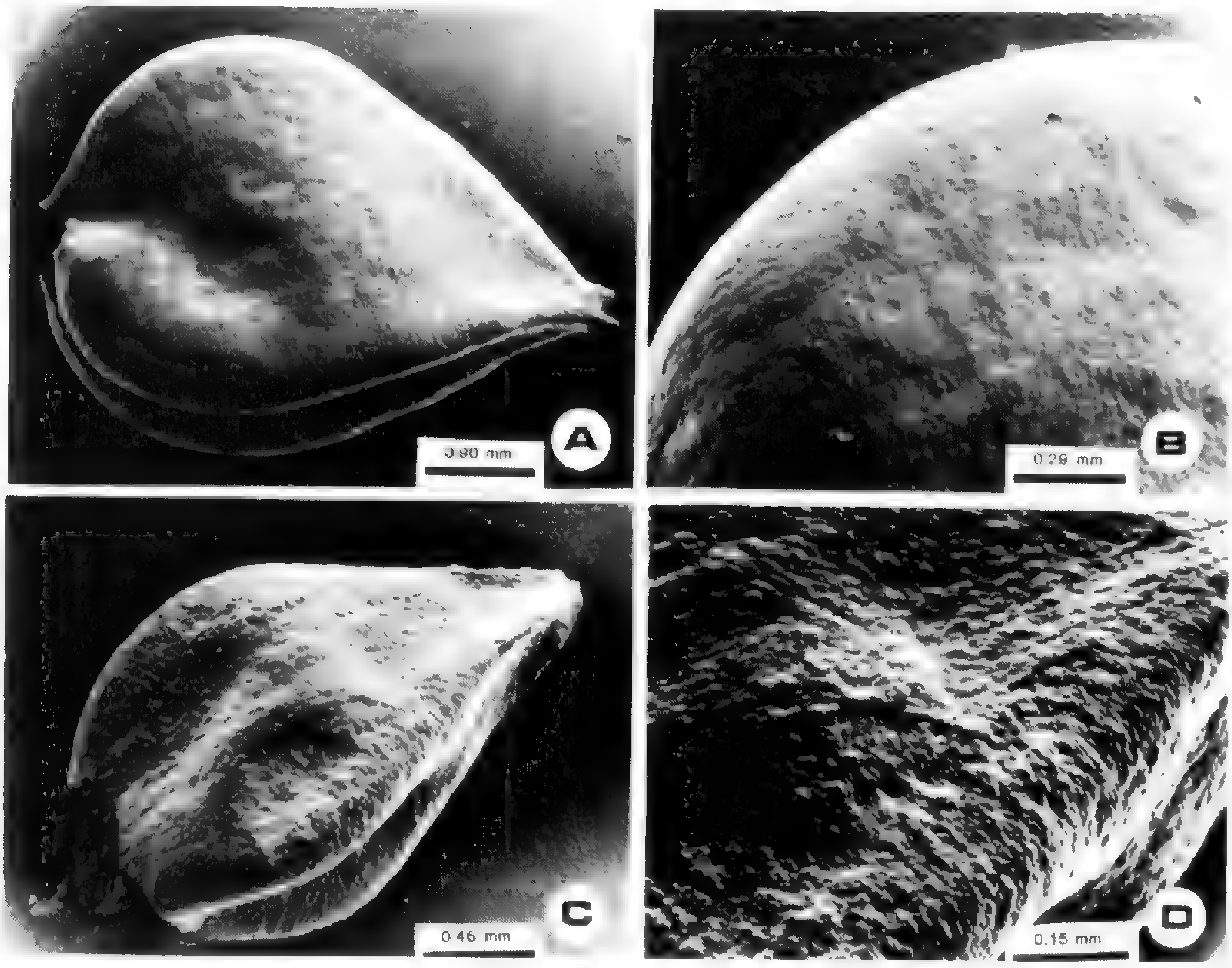


Figure 1. Scanning electron micrographs of *Polygonum* achenes. A & B: smooth type. C & D: roughened type.

KEY TO THE SPECIES OF *POLYGONUM* SECT. *POLYGONUM* IN CANADA

1. Achene smooth or somewhat roughened, never papillose.
  2. Achene smooth and shiny.
    3. Fruiting perianth white, at least at the margins, appearing ± petaloid, spreading at maturity; achenes 3.5–5 mm long, exserted; plants homophyllous, usually glaucous; maritime species .... **13.** *P. raii.*
    3. Fruiting perianth yellow-green throughout, appressed to achene at maturity; achenes 2–3.5 mm long, included; plants heterophyllous, glabrous; inland species, often weedy .... **14.** *P. ramosissimum.*
  2. Achenes irregularly roughened and dull.
    4. Leaves lanceolate, oblanceolate or linear, 5–12 times as long as broad.
      5. Plants heterophyllous; leaves acute; pedicels 2.5–3.5 mm long, exserted from the ochreae .... **14.** *P. ramosissimum.*

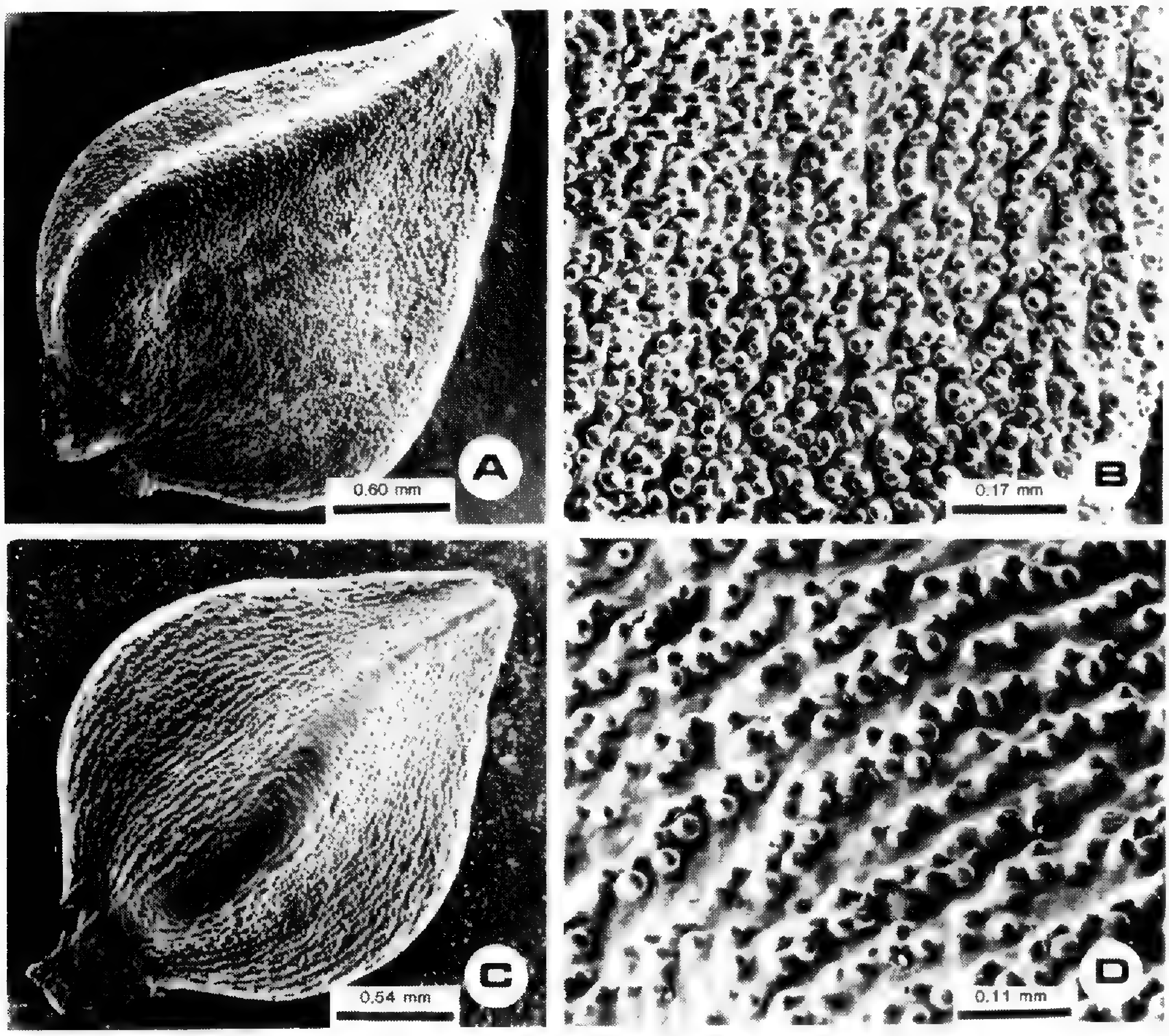


Figure 2. Scanning electron micrographs of *Polygonum* achenes. A & B: papillose type. C & D: striate-papillose type.

5. Plants homophyllous; leaves obtuse; pedicels 2 mm long, included in the ochreae .... **12.** *P. prolificum.*
4. Leaves oblong, ovate or obovate, 2–4 times as long as broad.
6. Achenes 3–4 mm long, beaked, with 3 sub-equal concave sides; fruiting perianth with cucullate tips enclosing achene at maturity; leaves 1–5 cm long, elliptic to elliptic-obovate, acute to obtuse; plants much branched throughout .... **9.** *P. fowleri.*
6. Achenes 1.5–2.5 mm long, beakless, with 1 narrow concave and 2 broad ± convex sides; fruiting perianth flat or flared at tip, rarely cucullate, the achene generally exserted at maturity; leaves less than 1.5 cm long, obovate, rounded to obtuse; plants branching mainly at the base .... *P. caurianum.*

7. Achenes 1.5–2.2 mm long; perianth lobes flared at maturity; plants of Mackenzie District, N. W. T., westward to Alaska .... **6.** ssp. *caurianum.*
7. Achenes 2–2.5 mm long; perianth lobes overlapping at maturity; plants of Hudson's Bay eastward to the St. Lawrence estuary .... **7.** ssp. *hudsonianum.*

1. Achenes papillose, the papillae visible at 30× magnification.
  8. Achene uniformly papillose, yellow-green to tan; fruiting perianth divided 1/3 or less to the base ...... **1.** *P. achoreum.*
  8. Achene striate-papillose, chestnut to dark brown; fruiting perianth divided 1/2 or more to the base.
    9. Plants heterophyllous.
      10. Leaves ovate-lanceolate to narrowly elliptic, acute; plants prostrate; ochreae brown, lacerate .... **3.** *P. aviculare.*
      10. Leaves elliptic to ovate, obtuse; plants erect; ochreae silvery, entire .... **8.** *P. erectum*
    9. Plants homophyllous.
      11. Leaves linear to lanceolate, 5–9 times as long as broad. .... **11.** *P. neglectum.*
      11. Leaves oblong, ovate or obtuse, 2–4 times as long as broad.
        12. Achenes with 3 convex sides; perianth tips cucullate; ochreae silvery, largely entire; lower stems somewhat woody .... **5.** *P. buxiforme.*
        12. Achenes with 1 narrow concave and 2 convex sides; perianth tips flat or flared, not cucullate; ochreae brown, lacerate; lower stems often wiry, but not woody.
          13. Achenes 2.4–2.8 mm long .... **4.** *P. boreale.*
          13. Achenes 1.5–2.2 mm long.
            14. Fruiting perianth divided to below the middle, the segments usually overlapping; leaves narrowly elliptic, 10–25 mm long; native species of shores and beaches of eastern Canada...................................... **10**. *P. franktonii.*
            14. Fruiting perianth divided to the middle or less, the segments rarely overlapping; leaves elliptic-oblanceolate, 5–20 mm long, widespread weedy species of dry disturbed areas .... **2.** *P. arenastrum.*

1. **Polygonum achoreum** Blake

Plants erect, homophyllous, glabrous, often whitish from powdery mildew infection; stems moderately branched, mostly from near the base, the branches mostly ascending, somewhat woody near the base, up to 50 cm long. Leaves short petiolate, oval to elliptic, apex rounded, 8–35 mm long. Ochreae 4–10 mm long becoming brown and lacerate. Inflorescence 1–3 flowered. Fruiting perianth 2.6–3.5 mm long, divided less than 1/3 to the base, the segments overlapping, the margins yellow to green, the apices cucullate. Achene 2.4–3.3 mm long, yellow-green to tan, uniformly papillose, with 1 narrow concave and 2 broad ± convex sides, included in the persistent perianth. Late-season fruits common, exserted, up to 5 mm long, olivaceous, smooth.

DISTRIBUTION: Very common in disturbed areas such as roadsides and sidewalks, throughout temperate Canada.

CHROMOSOME NUMBER: $2n = 40, 60$.

ACHENE TYPE: Papillose.

Polygonum achoreum is one of the most common and distinctive members of *Polygonum* section *Polygonum* and is almost certainly native as suggested by Fernald (1950). It is characterized by its elliptic, rounded leaves; distinctive yellow-green, bottle-shaped fruiting perianth which is divided 1/3 to the base or less; and its yellow-green to tan, uniformly papillose achenes which have one narrow and two broad convex sides. The only species with which it has been confused is *P. erectum*. Löve and Löve (1982) considered *P. achoreum* a subspecies of *P. erectum* and Mertens and Raven (1965) considered it synonymous with the latter. However, except for the erect habit and broad leaves of these two species, they bear little resemblance to each other. They differ with respect to achene size, shape, color and surface texture as well several features of the fruiting perianth and ochreae. In particular, *P. erectum* has conspicuous silver ochreae, striate-papillose achenes with three concave sides, and a very deeply divided fruiting perianth. In addition, *P. achoreum* is homophyllous while *P. erectum* is markedly heterophyllous.

2. **Polygonum arenastrum** Boreau

Plants prostrate, homophyllous, forming dense mats, glabrous; stems densely branched, 5–50 cm long. Leaves subsessile, elliptic to oblanceolate, acute to obtuse, 5–20 mm long, all approximately equal in size. Ochreae to 4 mm long, becoming brown and lacerate. Inflorescence 2–3 flowered. Fruiting perianth 1.8–2.6 mm long, the segments divided 1/2 way to the base, rarely overlapping, the margins white to pink, the apices flat. Achene 1.6–2.2 mm long, dark brown, striate-papillose, with one narrow concave and two broad convex sides, the tips slightly exserted from persistent perianth. Late season fruits common, prominently exserted from the perianth, up to 4 mm long, olivaceous, smooth.

DISTRIBUTION: Common in such disturbed sites as roadsides, vacant lots and sidewalks throughout most of temperate Canada.

CHROMOSOME NUMBER: $2n = 40$.

ACHENE TYPE: Striate-papillose.

Polygonum arenastrum is the most common member of *Polygonum* section *Polygonum* and was probably introduced from Europe (McNeill, 1981). It is characterized by its prostrate, matted habit, homophyllous leaves, striate-papillose achenes with one narrow concave and two broad convex sides, and fruiting perianth in which the segments are divided 1/2 way to the base and do not overlap. It is readily distinguished from *P. aviculare* and *P. buxiforme* by achene size and shape as well as several features of the fruiting perianth. Additionally, *P. aviculare* is heterophyllous and *P. buxiforme* has conspicuous, silver ochreae and a relatively thick and woody stem.

3. **Polygonum aviculare** L.

Plants prostrate to sub-erect or loosely spreading, heterophyllous, glabrous; stems freely branched, up to 2 m long. Leaves short-petiolate to subsessile, ovate-lanceolate to narrowly elliptic, acute, the largest on the main stem 25–60 mm long, progressively reduced on the branches. Ochreae 4–8 mm long, becoming brown and lacerate. Inflorescence 3–6 flowered, mostly restricted to the axils of upper reduced leaves. Fruiting perianth 2.9–4.0 mm long, the segments divided 3/4 to the base, overlapping, the margins white to pink, the apices flat. Achene 2.2–3.0 mm long, dark brown, striate-papillose, with three ± subequal concave sides, the tip ± slightly exserted from the persistent perianth. Late-season exserted fruits very rare.

DISTRIBUTION: Common on such disturbed sites as roadsides, vacant lots and sidewalks throughout most of temperate Canada.

CHROMOSOME NUMBER: $2n = 40, 60$.

ACHENE TYPE: Striate-papillose.

Polygonum aviculare is a common, introduced weed throughout most of temperate Canada. Its distinctive features have been enumerated in a number of studies (Styles, 1962; Mertens and Raven, 1965; McNeill, 1981). It is a heterophyllous species with striate-papillose achenes that have three sub-equal sides, and a deeply divided perianth in which the segments overlap in fruit. Additionally, the flowers are generally restricted to the upper portions of the branches, in the axils of reduced leaves. The heterophyllous habit, distinctively shaped achenes and perianth, and distinctive inflorescence of *P. aviculare* readily distinguish it from the other species of the section, particularly *P. arenastrum,* with which it is most often confused.

4. **Polygonum boreale** (Lange) Small

Plants prostrate, homophyllous, glabrous; stems sparsely branched, 3–25 cm long. Petioles less than 3 mm long, leaves obovate, acute, 5–20 mm long. Ochreae 1–3 mm long, silver-brown, slightly lacerate. Inflorescence 2–5 flowered. Fruiting perianth 2.8–3.5 mm long, the segments divided 3/4 to the base, overlapping, the margins white to pink, the apices flat. Achenes 2.4–2.7 mm long, dark brown, striate-papillose, with one narrow concave and two convex sides, the tips slightly exserted. Late-season fruits unknown.

DISTRIBUTION: Known from Greenland, but probably also present in boreal eastern Canada.

CHROMOSOME NUMBER: $2n = 40$.

ACHENE TYPE: Striate-papillose.

We, like Mertens and Raven (1965), are unable to account for this taxon in North America; however, since it occurs in Greenland, it can probably be expected to occur in boreal Canada. Fernald (1950) and Löve and Löve (1956) recognized it in North America; Gleason (1952) however, did not. Styles (1962) gave its distribution as the British Isles, Greenland, Iceland and Northern Scandinavia, and suggested that North American plants also fit its description. Plants of this species are relatively diminutive, and some resemble *Polygonum arenastrum;* however, *P. boreale* differs from *P. arenastrum* in its sparsely branched habit, larger fruiting perianth in which the segments are deeply divided and overlap, and larger fruits. The name *P. boreale* has been erroneously applied to a much larger, heterophyllous taxon that has spathulate, long petiolate leaves, a much larger fruiting perianth, and much larger achenes which have three concave sides (Fernald, 1959; Löve and Löve, 1956; Styles, 1962). However, we have examined Lange's type of *P. boreale* and are unable to account for Styles' (1962) description of this taxon. *Polygonum boreale sensu* Lange is homophyllous with obovate short petiolate leaves, a smaller fruiting perianth, and smaller striate-papillose achenes which have one narrow concave and two convex sides. It is evident that these two taxa are considerably different and Styles' (1962) concept of *P. boreale* is not congruent with Lange's original concept of *P. boreale*. However, since Lange's name and type have priority and this species can probably be expected in Canada, we have included it in this treatment.

5. **Polygonum buxiforme** Small

Plants prostrate, homophyllous, glabrous to slightly glaucescent; stems much branched, prominently ribbed, somewhat woody at lower nodes, up to 2 m long. Leaves distinctly short-petiolate, gray-glaucescent, subcoriaceous, obovate to oblanceolate, obtuse, 5–25 mm long. Ochreae to 5 mm long, hyaline-silvery, entire to only slighlty lacerate. Inflorescence 2–6 flowered. Fruiting perianth 2–3 mm long, divided 2/3 to 3/4 to the base, the segments overlapping, the margins white to pink, the apices cucullate, lower perianth asymmetric with a pouch-like protrusion. Achene 2.0–2.8 mm long, dark brown, striate-papillose, with three concave sides, one side slightly broader and the achene thus appearing heart-shaped, wholly included in the persistent perianth. Late-season fruits common, prominently exserted, up to 4.5 mm long, olivaceous, smooth.

DISTRIBUTION: Relatively common in disturbed sites such as roadsides, vacant lots, and sidewalks throughout most of temperate Canada, particularly the Prairie Provinces.

CHROMOSOME NUMBER: $2n = 60$.

ACHENE TYPE: Striate-papillose.

Polygonum buxiforme is a common and distinctive native, weedy species which heretofore had only been recognized in local floras (Savage and Mertens, 1968; Mitchell and Dean, 1978). It is characterized by its rather stout, somewhat woody stem, gray-glaucescent, sub-coriaceous, obovate, distinctly petiolate leaves, very deeply divided perianth which has cucullate apices and a pouch-like protrusion; and striate-papillose, heart-shaped achenes. It is readily distinguished from *P. aviculare* by its homophyllous habit and from *P. arenastrum* by its distinctively shaped achenes and fruiting perianth. In the Atlantic Provinces, *P. buxiforme* is sometimes confused with *P. fowleri;* however, the latter has roughened rather than striate-papillose achenes, and occurs on maritime beaches rather than on dry, disturbed sites.

6. **Polygonum caurianum** Robins. ssp. **caurianum**

Plants prostrate, homophyllous, glabrous, frequently purple; stems filiform, moderately branched mostly from the base, 2–15 (20) cm long. Leaves short petiolate, greenish-purple, elliptic, rounded to obtuse, 3–12 mm long. Ochreae less than 3 mm long, brown, lacerate. Inflorescence 2–6 flowered. Fruiting perianth 1.6–2.3 mm long, the longest segments 1.0–1.6 mm long, divided at least 2/3 to the base, rarely overlapping, the margins purple, the apices flat and flared. Achene 1.5–2.2 mm long, dark brown to purple, roughened, with one narrow concave and two broad, ± convex sides, exserted. Late season fruits common, exserted, up to 3.5 mm long, elongated, olivaceous to purple, smooth to roughened.

DISTRIBUTION: Relatively common on gravel bars and waste places, Mackenzie District, Northwest Territory westward through Alaska.

CHROMOSOME NUMBER: Unknown.

ACHENE TYPE: Roughened.

This distinctive taxon is relatively common from the Mackenzie District, N. W. T. westward through Alaska. It is distinguished by its diminutive habit, filiform stems, purple color, branching from the base, relatively small fruiting perianth and small, roughened achenes. Although it may appear similar to *Polygonum arenastrum, P. caurianum* ssp. *caurianum* is distinguished by its deeply divided perianth, roughened achenes, purple color and filiform habit. In addition to geographical distribution, ssp. *caurianum* is distinghished from ssp. *hudsonianum* by its smaller stature, achenes, fruiting perianth, leaves and petioles, its filiform stems and its non-overlapping, purple perianth segments with their flat and flared tips. The only other species in the region that ssp. *caurianum* could be confused with is *P. fowleri;* however, this species has much larger, beaked achenes with three concave sides and a much larger fruiting perianth with cucullate tips.

7. **Polygonum caurianum** Robins. ssp. **hudsonianum** S. J. Wolf & McNeill, *ssp. nov.* TYPE: QUEBEC, CANADA, Fort George, Baie James, Rampant, terrasse de sable, sec, 30 Aout 1950, *E. Lepage 12863,* DAO (Figure 3).

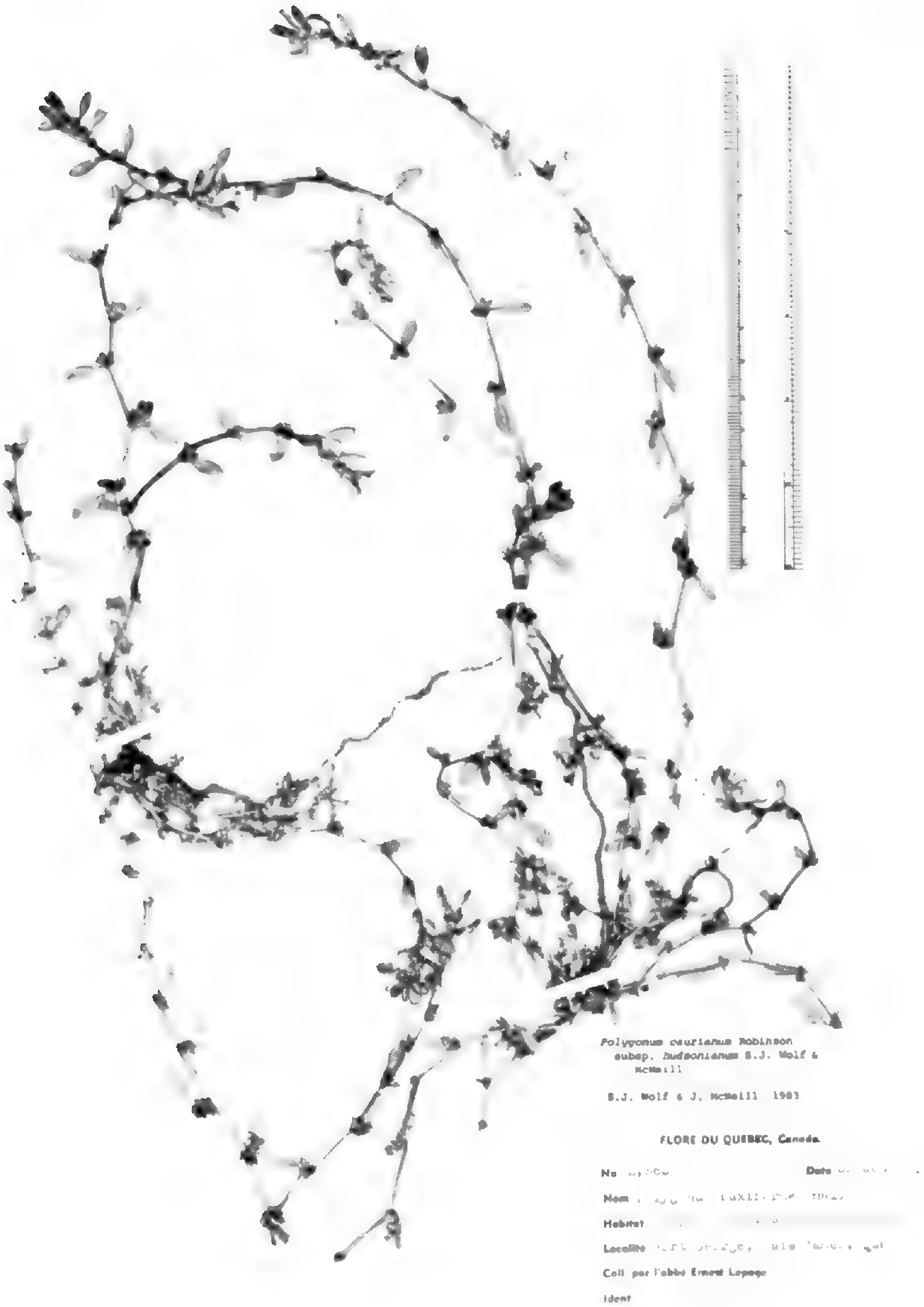


Figure 3. Holotype of *Polygonum caurianum* ssp. *hudsonianum* S. J. Wolf & McNeill.

Plantae prostratae, isophyllae, glabrae virides usque vix rubentes; caules aliquantum crassi, modice ramosi pro parte maxima e basi, 6–30 cm longi, internodiis comparate longis. Folia viridia usque rubentia, elliptica usque angusto-obovata, rotundata usque obtusa, 6–20 mm longa, basi saepe in petiolum distinctum attenuata. Ochreae minus quam 3 mm longae, hyalinae usque brunneae, vix laceratae. Inflorescentia 2–6 floribus praedita. Perianthium in fructu 2.6–3.3 mm longum, segmentis longis 1.3–2.1 mm longissimis, 2/3 – 3/4 ad basim fissis, imbricatis, marginibus albis usque roseis, apicibus planis usque vix cucullatis. Achenium 2.0–2.5 mm longum, fuscum, exasperatum, lateribus duobus latis ± convexis et uno latere angusto concavo, pro parte maxima exsertum; fructus temporis serotini abundantes, ad 4.5 mm longi, elongati, olivacei usque brunnei laeves usque exasperati. Chromosomatum numerus ignotus.

Plants prostrate, homophyllous, glabrous, green to slighlty reddish; stems relatively stout, moderately branched, mostly from the base, 6–30 cm long, internodes relatively long. Leaves green to reddish, the base frequently tapering to a distinct petiole up to 4 mm long, elliptic to narrowly obovate, rounded to obtuse, 6–20 mm long. Ochreae less than 3 mm long, hyaline to brown, slightly lacerate. Inflorescence 2–6 flowered. Fruiting perianth 2.6–3.3 mm long, the longest segments 1.3–2.1 mm long, divided at least two thirds to the base, overlapping, the margins white to pink, the apices flat to somewhat cucullate. Achene 2.0–2.5 mm long, dark brown, roughened, with one narrow concave and two broad ± convex sides, mostly exserted. Late-season fruits very common, exserted, up to 4.5 mm long, elongated, olivaceous to brown, smooth to roughened.

DISTRIBUTION: Relatively uncommon on gravelly shores, Hudson and James Bays, eastward to Labrador and the St. Lawrence estuary.

CHROMOSOME NUMBER: Unknown.

ACHENE TYPE: Roughened.

This new subspecies of *Polygonum caurianum* is relatively uncommon and occurs from Hudson and James Bays eastward to Labrador and the St. Lawrence estuary. Although Hultén (1968) did not recognize this taxon, his distribution map of *P. caurianum* from Hudson Bay eastward reflects most of its known distribution. *Polygonum caurianum* ssp. *hudsonianum* also occurs in northern Quebec and Labrador (see distribution map of *P. caurianum*, Porsild and Cody, 1980). Based on Fernald's (1950) description and distribution of *P. boreale*, particularly in Cote Nord, Quebec and the shores of Hudson Bay, we suspect that *P. caurianum* ssp. *hudsonianum* is at least partly included in his concept of *P. boreale*. In addition to its geographical distribution, ssp. *hudsonianum* is distinguished from ssp. *caurianum* by a number of chiefly quantitative features including its larger stature, achenes, fruiting perianth and leaves, longer petioles, stouter stems and overlapping, white to pink perianth segments which have slightly cucullate tips. Additionally, ssp. *hudsonianum* has a large number of elongated late-season fruits, even in early August. As Davis and Heywood (1963) note, subspecies are chiefly differentiated by a number of largely quantitative characters, usually in conjunction with geographical discontinuities. We therefore feel it appropriate to recognize the eastern race of *P. caurianum* at the subspecific level.

8. **Polygonum erectum** L.

Plants erect, heterophyllous, glabrous; stems stout, up to 75 cm long, sparingly branched, with relatively long internodes. Petioles distinct, less than 4 mm long; leaves elliptic to obovate, obtuse, the largest on the main stems 25 60 mm long, shorter on the branches. Ochreae 5–10 mm long, hyaline-silvery, entire to slightly lacerate. Inflorescence 2–3 flowered. Fruiting perianth 2.8–3.2 mm long, the segments divided 3/4 to the base, overlapping, yellow-green, the tips cucullate. Achene 2.4–3.0 mm long, light to dark brown, striate-papillose, with three ± equal concave sides, wholly enclosed by the persistent perianth. Late-season fruits uncommon, exserted, up to 5 mm long, olivaceous, smooth.

DISTRIBUTION: A very rare species of waste places across Canada, but particularly localized in southern Ontario and central Alberta.

CHROMOSOME NUMBER: Unknown.

ACHENE TYPE: Striate-papillose.

Polygonum erectum is a rare but distinctive native species frequently confused with *P. achoreum.* Most collections of *P. erectum* in Canada and the eastern United States are pre-twentieth century, with a few from the 1940's and 1950's. It is distinguished by its erect, heterophyllous habit; broad leaves; conspicuous, silver ochreae; deeply divided perianth and striate-papillose achenes. Most herbarium specimens labeled *P. erectum* are actually *P. achoreum;* for example, the vouchers for published chromosome counts of *P. erectum* at BSUH by Moore *et al.* (1970) are in fact *P. achoreum.* Löve and Löve (1982) considered these taxa to be related and treated them as subspecies of *P. erectum.* Mertens and Raven (1965) could make no distinction between the two and therefore considered *P. achoreum* synonymous with the earlier *P. erectum*. However, although superficially similar in habit, the two species differ with respect to achene shape, size, color and surface texture, as well as in their ochreae and fruiting perianth. The heterophyllous habit, striate-papillose achenes with three concave sides, and deeply divided fruiting perianth of *P. erectum* contrast with the homophyllous habit, uniformly papillose achenes with one concave and two convex sides, and slightly divided fruiting perianth of *P. achoreum*.

9. **Polygonum fowleri** Robins.

Plants prostrate to ascending, homophyllous, sub-succulent, glabrous; stems moderately branched, up to 50 cm long. Leaves short petiolate, reddish to green, often sub-succulent, elliptic to elliptic-obovate, acute to obtuse, 10–45 mm long. Ochreae less than 4 mm long, lacerate, brown. Inflorescence 2–5 flowered, the pedicels included in the ochreae. Fruiting perianth 3.5–4.5 mm long, the segments divided 3/4 to the base and overlapping, the margins white to pink, the apices cucullate. Achene 3.0–4.0 mm long, beaked, chestnut to dark brown, roughened, with three sub-equal concave sides, wholly included in the persistent perianth. Late-season fruits common, much like normal fruits but with only the tip elongated, exserted, olivaceous to light brown, smooth to roughened.

DISTRIBUTION: Common on sandy or gravelly seashores on both the west and east coasts of Canda and the St. Lawrence estuary, but relatively rare in the southern Hudson and James Bay regions.

CHROMOSOME NUMBER: $2n = 40, 60$.

ACHENE TYPE: Roughened.

Polygonum fowleri is a common native species of both the west and east coasts of Canada. It is distinguished by its frequently sub-succulent habit, elliptic to elliptic-obovate leaves, deeply divided fruiting perianth with overlapping, cucullate segments, and relatively large, beaked, roughened achenes with three concave sides. *Polygonum fowleri* is relatively uncommon in the Hudson and James Bay regions, where it has been confused with *P. caurianum* ssp. *hudsonianum*. However, the latter is distinguished by its considerably smaller beakless achenes which have one narrow concave and two convex sides. *Polygonum buxiforme* is also sometimes confused with *P. fowleri;* however, the former has much smaller, beakless, striate-papillose achenes and conspicuous silver ochreae.

10. **Polygonum franktonii** S. J. Wolf & McNeill. *sp. nov.* TYPE: NOVA SCOTIA, CANADA, Digby County, coast road, St. Bernard to New Edinburg, *J. McNeill 5172,* 2 Sept. 1976, DAO (Figure 4).

Plantae erectae, isophyllae, glabrae; caules internodiis comparate longis, vix ramosi ramis plerumque a basi orientibus, 10–15 cm longi. Folia angusto-elliptica, acuminata, 10–25 mm longa; petioli ad 3 mm longi. Ochreae ad 6 mm longae, argenteae usque brunneae solum vix laceratae. Inflorescentia 2–3 floribus praedita. Perianthium in fructu 2.1–2.8 mm longum, segmentis 3/4 ad basin fissis, imbricatis, marginibus albis usque roseis, apicibus planis. Achenia 2.0–2.4 mm longa, fusca, striato-papillosa, lateribus duobus latis convexis et uno latere concavo praedita, apicibus vix exsertis. Fructus temporis serotini ignoti. Chromosomatum numerus $2n = 60$.

Plants erect, homophyllous, glabrous; stems with relatively long internodes, sparingly branched, mostly from near the base, 10–50 cm long. Petioles up to 3 mm long; leaves narrowly elliptic, acuminate, 10–25 mm long. Ochreae to 6 mm long, silver to brown, sublacerate. Inflorescence 1–3 flowered. Fruiting perianth 2.1–2.8 mm long; the segments divided 3/4 to the base, overlapping, the margins white to pink, the apices flat. Achenes 2.0–2.4 mm long, dark brown, striate-papillose, with one narrow concave and two broad convex sides, the tips slightly exserted. Late season fruits unknown.

DISTRIBUTION: Maritime and freshwater beaches, dunes and shores in eastern Canada.

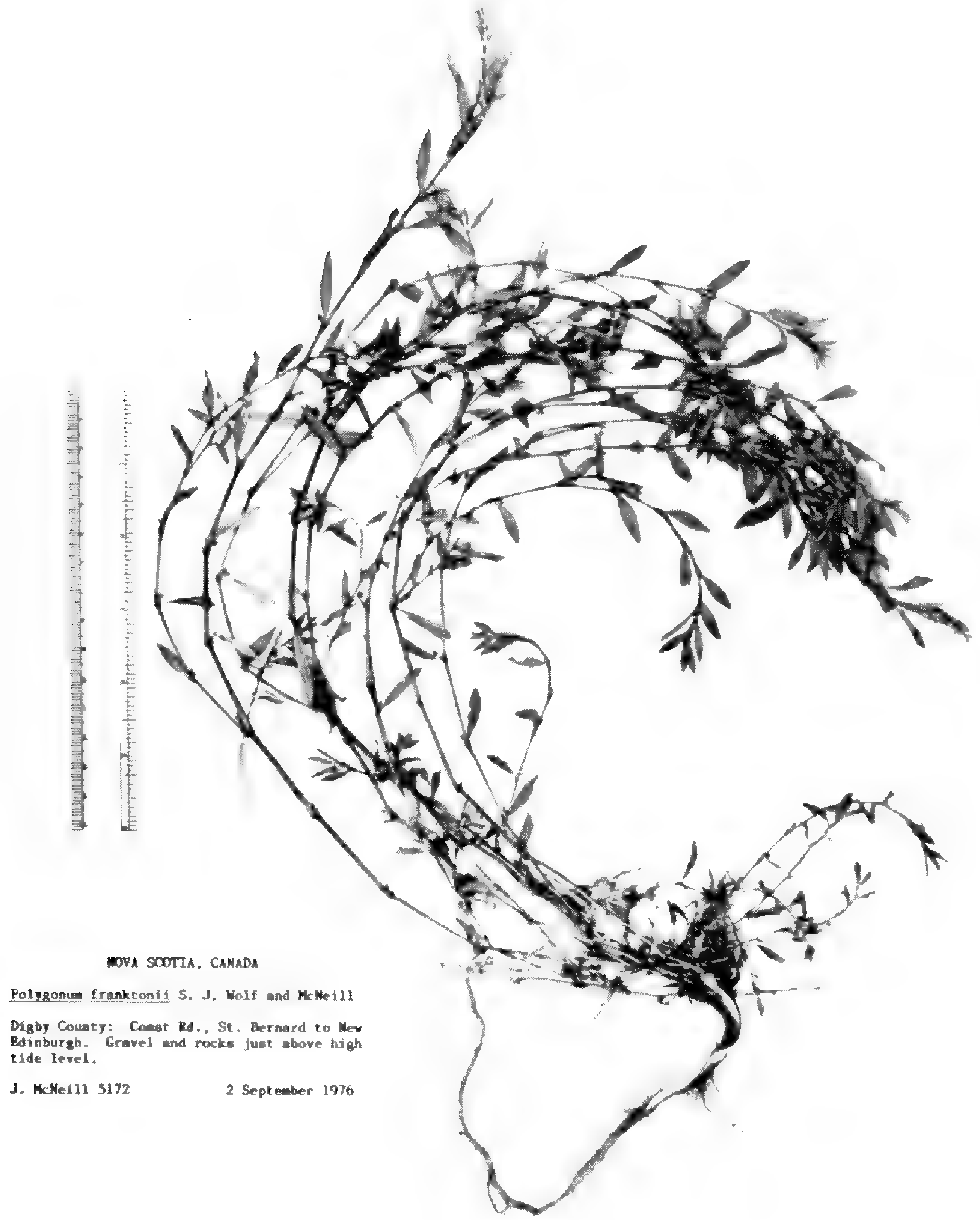
CHROMOSOME NUMBER: $2n = 60$.

ACHENE TYPE: Striate-papillose.

This distinctive new species, named for Clarence Frankton, is restricted to native habitats on beaches and shores in eastern Canada. It is an erect, homophyllous hexaploid with narrowly elliptic leaves and relatively long internodes. Although quite distinct, *Polygonum franktonii* shares some features with both *P. aviculare* and *P. arenastrum.* Its fruiting perianth, although shorter than that of *P. aviculare,* is deeply divided and the segments overlap. However, its achenes, which have one narrow concave and two broad convex sides, are similar to those of *P. arenastrum.*

11. **Polygonum neglectum** Besser

Plants prostrate to ascending, homophyllous, glabrous; stems slender, flexuous, sparingly branched, up to 50 cm long, internodes



NOVA SCOTIA, CANADA

Polygonum franktonii S. J. Wolf and McNeill

Digby County: Coast Rd., St. Bernard to New Edinburgh. Gravel and rocks just above high tide level.

J. McNeill 5172 2 September 1976

Figure 4. Holotype of *Polygonum franktonii* S. J. Wolf & McNeill.

relatively long. Petioles less than 2 mm long; leaves linear-lanceolate, acute, 8–30 mm long. Ochreae to 4 mm long, silver to brown, becoming lacerate. Inflorescence 2–3 flowered. Fruiting perianth 1.9–2.8 mm long, the segments divided 1/2 to 2/3 to the base, free, the margins white to pink, the apices flat. Achene 2.0–2.3 mm long, dark brown, striate-papillose, with one narrow concave and two broad convex sides, exserted from the persistent perianth. Late season fruits common, prominently exserted, up to 4.5 mm long, olivaceous, smooth.

DISTRIBUTION: Common in such disturbed sites as roadsides, vacant lots and sidewalks throughout most of temperate Canada.

CHROMOSOME NUMBER: $2n = 40, 60$.

ACHENE TYPE: Striate-papillose.

Polygonum neglectum is a relatively common and apparently native species that has usually been included in *P. arenastrum.* Fernald (1950), who recognized three varieties of *P. arenastrum,* considered *P. neglectum* the typical form while Mitchell and Dean (1978) recognized it at the specific level. Although *P. arenastrum* and *P. neglectum* are somewhat similar, *P. neglectum* differs by its more ascending, slender, relatively unbranched stems which have longer internodes, linear leaves, a slightly longer and more divided fruiting perianth, and larger achenes. Additionally, since *P. arenastrum* is uniformly tetraploid and introduced while *P. neglectum* is native and has both tetraploid and hexaploid chromosome races (Wolf and McNeill, 1986) we recognize it at the specific level.

12. **Polygonum prolificum** (Small) Robins.

Plants erect to ascending, homophyllous, glabrous; stems with numerous upcurving branches, 15–80 cm long. Leaves short petiolate, oblanceolate, rounded to obtuse, 8–30 mm long, green to bluish-green, rugose-veiny. Ochreae to 3 mm long, silver to brown, lacerate. Inflorescence 2–4 flowered, the pedicels less than 2 mm long, included within the ochreae. Fruiting perianth 2.2–2.8 mm long, the segments divided 3/4 to the base, overlapping, the margins white to pink, the apices cucullate. Achene 2.5 mm long, included in the persistent perianth, brown, roughened (occasionally smooth), with three subequal concave sides. Late season fruits common, exserted, up to 4 mm long, lanceolate, olivaceous, smooth.

DISTRIBUTION: Uncommon in waste places and saline shores throughout temperate Canada.

CHROMOSOME NUMBER: $2n = 60$.

ACHENE TYPE: Roughened.

Polygonum prolificum is a relatively uncommon native species which has often been confused with *P. ramosissimum.* Mitchell and Dean (1978) considered it a variety of the latter. However, *P. ramosissimum* is heterophyllous, considerably larger, yellow, has larger achenes and fruiting perianths, and very long exserted pedicels. In contrast, *P. prolificum* is homophyllous, smaller, and has rounded, veiny leaves, upcurved branches, roughened achenes and the flowers are not clustered in the upper branch tips.

13. **Polygonum raii** Bab.

Plants prostrate to erect, homophyllous, glaucescent to glacous and slightly fleshy; stems sparingly branched, mostly from the base, up to 75 cm long. Leaves short petiolate, lanceolate to narrowly elliptic, acute, 10–40 mm long. Ochreae to 5 mm long, brown, 3–5 nerved, lacerate. Inflorescence 2–6 flowered. Fruiting perianth 3.5–5.5 mm long, divided 3/4 to the base, the segments broadly petaloid and ± overlapping, the margins white to pink, the apices flat and flared. Achene 3.5–5 mm long, chestnut to brown, smooth, with three subequal concave sides, exserted. Late season fruits unknown.

DISTRIBUTION: Relatively common on maritime beaches, dunes and shores throughout Atlantic Canada.

CHROMOSOME NUMBER: $2n = 40$.

ACHENE TYPE: Smooth.

Polygonum raii is a distinctive maritime species of beaches and shores throughout Atlantic Canada. It is distinguished by it glaucous habit, very large petaloid perianth segments, and large smooth achenes. The only species it is likely to be confused with is *P. glaucum* which occurs farther south. However, the latter has narrow leaves, much smaller achenes and perianth, and much longer (up to 1 cm) 8–10 nerved ochreae.

14. **Polygonum ramosissimum** Michx.

Plants erect, heterophyllous, glabrous to sub-glaucescent, yellowish; stems moderately branched, prominently ridged, stiff, to 1.5 cm diameter at the base, to 2 m long. Leaves short petiolate, yellow-green, lanceolate, acute to acuminate, the largest on the main stem to 60 mm long, progressively reduced upward. Ochreae to 5 mm long, silver to brown, lacerate. Inflorescence 2–4 flowered, largely restricted to upper branches among reduced leaves; pedicels 2.5–3.5 mm long, exserted from the ochreae. Fruiting perianth 2.8–3.7 mm long, the segments divided 3/4 to the base and overlapping, the margins yellow-green, the apices cucullate. Achene 2.5–3.5 mm long, brown, smooth (rarely roughened), with three subequal concave sides, included in the persistent perianth. Late-season fruits very common, prominently exserted, up to 15 mm long, lanceolate, olivaceous, smooth.

DISTRIBUTION: Common in waste places, and particularly in saline soils and shores throughout temperate Canada, especially the Prairie Provinces.

CHROMOSOME NUMBER: $2n = 60$.

ACHENE TYPE: Smooth.

This very distinctive species is common throughout most of Canada, particularly the Prairie Provinces. Its erect, yellow, thick stems up to 2 meters tall; heterophylly; long, lanceolate leaves; long pediceled flowers restricted to the upper branches; and smooth achenes distinguish it from the other members of *Polygonum* section *Polygonum*. The only species it has been confused with is *P. prolificum,* which has been considered a variety of *P. ramosissimum* (Mitchell and Dean, 1978). However, *P. prolificum* is homophyllous, considerably smaller in stature, green, has smaller achenes and fruiting perianths, and very short pedicels included within the ochreae. The late season fruits of *P. ramosissimum,* up to 15 mm long, are the longest of any species in the section. We concur with Gleason (1952) and Mertens and Raven (1965) that *P. exsertum* is a late-season form of *P. ramosissimum.*

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DEPARTMENT OF BIOLOGY
UNIVERSITY OF OTTAWA
OTTAWA, ONTARIO K1N 6N5

RARE VASCULAR PLANTS OF GROS MORNE NATIONAL PARK, NEWFOUNDLAND, CANADA

André Bouchard, Stuart Hay, Claire Gauvin
and Yves Bergeron

ABSTRACT

In Gros Morne National Park, Newfoundland, 43 vascular plant taxa have been identified as significantly rare; they are examined in subgroups of species sharing similar special habitats. These divisions correspond to a general classification of land regions and biophysiographic areas characterizing the Park. Aspects of range pattern, floristic affinity, ecology and community composition of the populations are discussed within each subgroup. Information from sample populations is treated by principal coordinate ordination to illustrate relationships between rare plant communities and abiotic variables.

Key Words: Rare plants, biophysiographic areas, ordination, phytogeography, Gros Morne National Park, Newfoundland

INTRODUCTION

The west coast of Newfoundland has a well established reputation for its interesting vascular flora. The importance of this area was first recognized by Fernald in the early part of this century. His pioneering explorations led to many important discoveries related in the pages of Rhodora (Fernald, 1911, 1926–27, 1933) and resulted in two landmark papers concerning the phytogeography of the region (Fernald, 1924, 1925). The presence of so many special disjunct and endemic elements in the flora of this coast has raised exciting problems in plant geography which continue to stimulate discussion and provoke interpretation. Furthermore, when examined in the greater context of the Gulf of St. Lawrence region, the west coast of Newfoundland (Figure 1) harbours a high proportion of these critical taxa. Drury (1969), Morisset (1971) and Rousseau (1974) have surveyed the problems and hypotheses which have made this area the focus of attention of botanists and plant geographers for more than half a century.

Gros Morne National Park was created in 1973 to preserve the most significant and representative sector of the west coast of Newfoundland (Figure 2). The outstanding landscape features and important natural resources of the Park (Airphoto Analysis Assoc.,

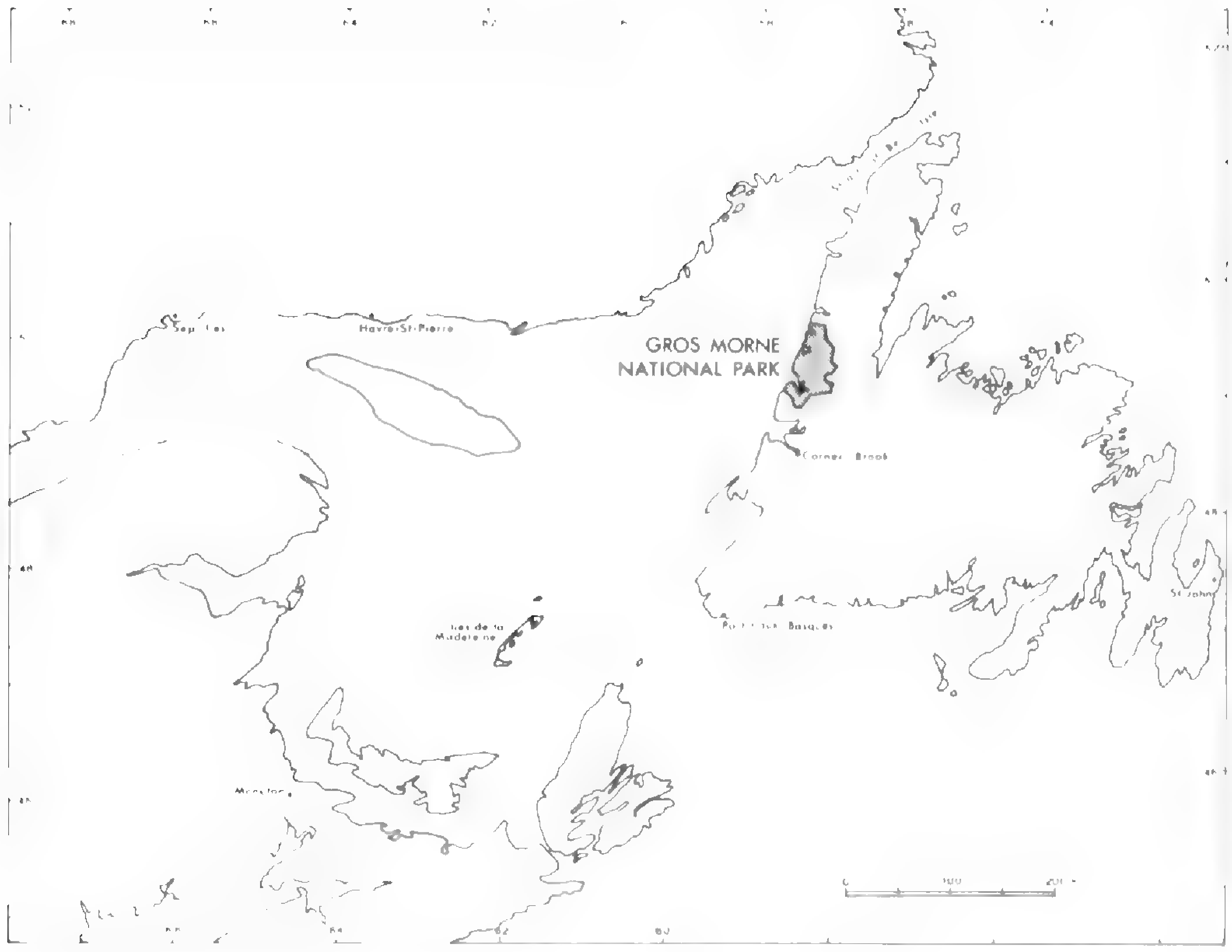

Figure 1. Location of Gros Morne National Park, Newfoundland, in the Gulf of St. Lawrence

1975; Bouchard, 1975) make this area one of the most distinctive parts of the Natural Land Region of Canada—Highlands of Western Newfoundland (Falkner & Carruthers, 1974).

Study and protection of rare plants have attracted considerable attention over the last decade. In North America, both Canada and the United States have embarked on programs of evaluation and preservation of their rare native flora. Since 1975, the Botany Division of the Museum of Natural Sciences of Canada has directed and published reports for eight provinces. Similarly, in eastern Canada, Forillon National Park, Québec (Morisset, P. 1974, 1979. Parks Canada report, Ottawa) and Cape Breton Highlands National Park (Hinds, H. 1982. Parks Canada report, Ottawa) have been the subject of unpublished reports on their rare vascular flora.

Identification and study of the rare plants of Gros Morne National Park were undertaken to underline their importance in the Newfoundland flora and to provide the basis for necessary protection, future park planning and nature interpretation.

PREVIOUS FLORISTIC STUDIES

The western coast of Newfoundland has attracted many notable botanists. Bachelot de la Pylaie, a French naturalist, made two trips to Newfoundland (Leroy, 1957), the first in 1816 and the second in 1819–20. He spent fifteen days at St. Georges's Bay and eight days at Ingornachoix. This first locality is south and the latter is north of Gros Morne National Park. Unfortunately the vascular plant section of his flora was not published, but his important herbarium collections are kept at the National History Museum of Paris. At the end of the last century, A. C. Waghorne did some collecting in regions southeast of the park area. His findings and studies of other botanists were published in the form of a flora (Waghorne, 1893, 1895, 1898).

In the first part of this century M. L. Fernald directed a series of botanical trips in western Newfoundland. Within Gros Morne National Park, his explorations were limited mainly around Bonne Bay where he made a remarkable contribution to our knowledge of the flora and was the first to find 20 of the Park's 43 rare vascular plants. Many of these rare and localized plants of western Newfoundland and of other areas in the Gulf of St. Lawrence, especially endemic and disjunct elements, were the basis for his famous nunatak theory, discussed in "Persistence of plants in unglaciated areas of Boreal America" (Fernald, 1925).

Another important contribution to the knowledge of the flora of Newfoundland was made by E. Rouleau of the Université de Montréal. In addition to collecting herbarium specimens from all over the province, he compiled previous collection records and prepared distribution maps. He published three checklists of the vascular plants of Newfoundland (Rouleau, 1949, 1956, 1978); he discovered two of the Park's rare vascular plants.

During this same period, other botanists such as Elkington, Janson, Kimball and Penson discovered seven more of the rare vascular plants in the Park. Creation of Gros Morne National Park favoured further botanical studies carried on by our research group (Bouchard et al., 1977, 1978; Bouchard & Hay, 1974, 1976a, b); discovery of fifteen of its rare plants resulted from these studies.

METHODOLOGY AND CRITERIA

An approach similar to that developed for the "Rare Vascular Plants of Québec" (Bouchard et al., 1983) was employed. An exhaustive listing of all the vascular plants known from Gros Morne National Park was extracted from the "Flora of St. Barbe South District" (Bouchard et al., 1978). This information was amended with more recent revisions and additions. Working from this catalogue, each taxon was examined for potential rarity. The great majority was quickly excluded from further consideration for the following reasons: common or evidently widespread taxa, introduced alien species or varieties, hybrid taxa, misidentified specimens, and names which have been placed in synonymy with more widespread or common species. Following this initial screening, all taxa on the residual list of candidates were evaluated in order to select the most significant or exceptional rare elements in the flora of Atlantic Canada. Two general categories exist: (a) those species of very restricted distribution such as endemic and disjunct elements, and (b) species at the limit of their native range or species showing a more widespread distribution, but which occur only in disparate, localized colonies in Newfoundland.

We consider all of the 43 species treated as rare in Gros Morne to be rare for Newfoundland. It is noteworthy that 39 of these plants have also been designated as rare in other provinces, states or Gulf of St. Lawrence National Parks.

All published information concerning the flora of Newfoundland was considered in evaluating the rare status of the selected plants. The distribution maps of the island's flora, compiled by E. Rouleau (unpublished files at the Marie-Victorin Herbarium, Université de Montréal), were especially useful at this stage. Particular attention was paid to the west coast because of the unique flora associated with the limestone or serpentine bedrock and the arctic-alpine element found on the Long Range Plateau of the Northern Peninsula.

Fieldwork in late July and early August of 1984 permitted us to locate and sample populations of 39 of these rare plants, with the objective of describing the community and the habitat for each population. Some additional sampling information concerning numbers of colonies, surface area occupied, slope, aspect, and altitude has been compiled (Bouchard et al., 1985a, and CISTI[1]).

At each site, soils were sampled for pH, cation exchange capacity, base concentration, organic carbon, total nitrogen, conductivity, and exchangeable H and Al following standard procedures (McKeague, 1978; Thomas, 1982).

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[1] Depository of Unpublished Data, CISTI, National Research Council of Canada, Ottawa, Ont., Canada K1A 0S2

Species are here grouped to correspond to the classification of general biophysiographic areas of the Park which have been earlier defined for analysis of the entire vascular flora (Bouchard et al., 1978, 1985b). Descriptive profiles resuming total range, Newfoundland distribution, pertinent published maps, general habitat and rare status in North America for the 43 rare taxa are contained in an Appendix which has been deposited at CISTI. This Appendix also includes a complete bibliography and the list of voucher specimens (Bouchard et al., 1985a), compiled from the following herbaria, BM, CAN, DAO, GH, MT and NFLD. Nomenclature followed is taken from the "Vascular Flora of Gros Morne National Park" (Bouchard et al., 1985b), based largely on Scoggan (1978–79), with updated synonymy following Kartesz and Kartesz (1980).

To study the relationships between rare plant communities, an ordination of rare plant stands, based on presence and absence of associated species, was performed using principal coordinate analysis (Gower, 1966) on a similarity matrix computed with Jaccard's coefficient (Legendre & Legendre, 1983). The ordination techniques were selected because of their performance at high β diversity, as was the case with our data. The two first axes, representing respectively 10% and 8% of the total variablility, were used for interpretation. Spearman's rank correlations (Nie et al., 1975) between abiotic variables and rare plant stand positions were computed for this purpose.

RESULTS AND DISCUSSION

The 43 rare vascular plants of Gros Morne National Park are distributed in the four land regions comprising different biophysiographic units (Bouchard et al., 1978, 1985b) of the Park territory as follows: Coastal Plain (11), Limestone Escarpments (12), Alpine Plateau (15), and Serpentine Tableland (5).

Coastal Plain

On the coastal plain, 11 rare vascular plants are found within the following biophysiographic units: tidal flats and brackish shores, peatlands, and freshwater areas.

Tidal Flats and Brackish Shores

In this biophysiographic unit, the rare species *Solidago sempervirens* L. and *Zannichellia palustris* L. (halophytic plants with widespread distributions, particularly southward along the Atlantic

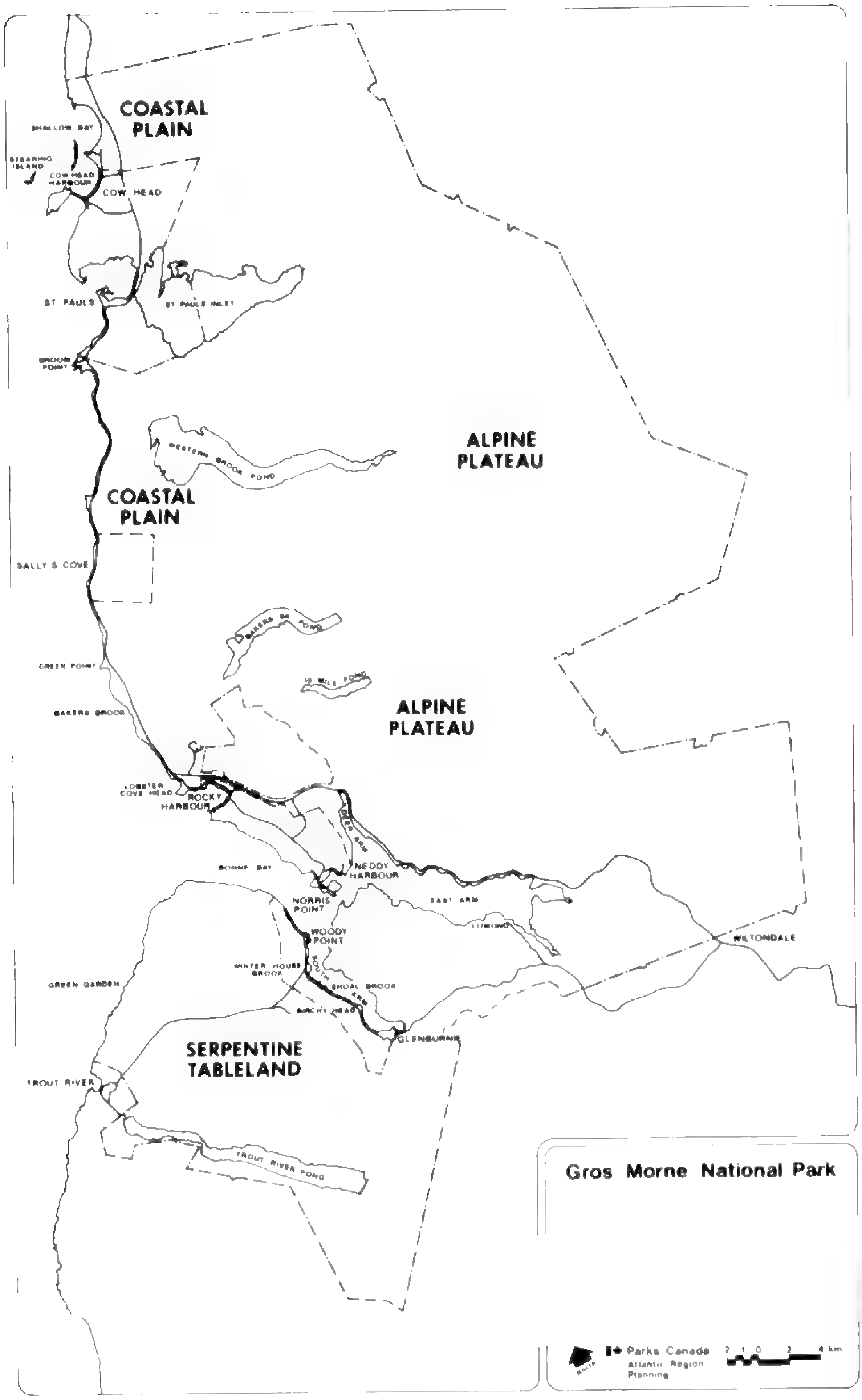

Figure 2. Gros Morne National Park

seaboard) reach the northern limit of their distribution and are known from only a few widely scattered localities. A third rare species, *Elymus virginicus* L., is also included in this category because the Bonne Bay plants are referable to *E. virginicus* var. *halophilus* (Bickn.) Wieg., a halophytic variety found along the Atlantic seacoast.

As described by Bouchard et al. (1978), the only saltmarsh, tidal-flat or well-developed brackish shoreline communities in the Park occur in the eastuaries around the arms of Bonne Bay and in part of St. Pauls Inlet. No populations of these plants have been located north of Bonne Bay.

Of the three rare species, only *Zannichellia palustris* is a true aquatic, occurring in tidal pools in the species-poor tidal mud-flats. *Elymus virginicus* and *Solidago sempervirens* occur in sporadic populations on brackish sand or gravel strands. Despite the fact that these sites are influenced by sea water, salinity as measured by conductivity (Jackson, 1958) is relatively low. This finding can be explained by fresh water seepage in the wet shoreline habitats and by leaching in the dry habitats such as gravel strands. Some stands seem to be more stabilized with presence of humus accumulation while others are unstable habitats with low organic accumulation (Bouchard, et al., 1985a). Colonies are found at very few sites and the plants occur in low numbers, along with the common characteristic maritime species *Glaux maritima* L., *Ligusticum scoticum* L., *Plantago maritima* L. and *Triglochin maritima* L. Admixed are the aggressive widespread adventives *Agropyron repens* (L.) Beauv., *Agrostis stolonifera* L. and *Festuca rubra* L.

Peatlands

The six rare vascular plants of the peatlands, *Cypripedium reginae* Walt., *Drosera linearis* Goldie, *Eriophorum gracile* W. D. J. Koch, *Parnassia glauca* Raf., *Rhynchospora capillacea* Torr., and *Salix serissima* (Bailey) Fern., are widespread mostly boreal species that are either transcontinental or have important western ranges from Alberta or Saskatchewan to Newfoundland. *E. gracile* is also found in Eurasia.

The six rare vascular plants were found mainly in eutrophic and very poorly drained sites such as American larch scrub and sedge fens (Bouchard et al., 1985a). Although oligotrophic bogs are common in Gros Morne National Park, eutrophic peatlands are rather scarce. These plant communities are relatively rich, containing many species such as *Habenaria dilatata* (Pursh) Hook. [*Platanthera dilatata* (Pursh) Lindl. *ex* Beck var. *dilatata*], *Potentilla fruticosa* L., *Primula mistassinica* Michx., *Rhamnus alnifolia* L'Hér., and *Thalictrum pubescens* Pursh. Several other eutrophic sites were sampled which lacked these rare plants. *Eriophorum gracile* seems to occupy a more acidic (pH 4.8) microhabitat with associated seepage from serpentinic soils (Ca: Mg ratio 0.51; Bouchard et al., 1985a).

These six plants are all found within slowly evolving plant communities that should maintain their present composition and structure.

Freshwater Areas

The two rare vascular plants of the aquatic communities, *Potamogeton amplifolius* Tuckerm. and *Ranunculus hyperboreus* Rottb., are widespread transcontinental species. *R. hyperboreus,* which also occurs in Greenland and Eurasia, has not been observed in Gros Morne since its discovery in 1940 by Penson. *P. amplifolius* is a subdominant of an aquatic plant community dominated by *P. epihydrus* Raf. and *Sparganium angustifolium* Michx. [*S. emersum* Rehmann] (Bouchard et al., 1985a). This well-established community colonizes one shallow acidic pond with a muddy or rocky bottom located on the coastal plain.

Limestone Escarpments

Gros Morne National Park is especially rich in rare calcicolous vascular plants. In the limestone escarpment land region are found *Androsace septentrionalis* L., *Antennaria cana* (Fern. & Wieg.) Fern. [*A. alpina* (L.) Gaertn. var. *media* (Greene) Jepson], *A. gaspensis* (Fern.) Fern. [*A. neglecta* Greene var. *gaspensis* (Fern.) Cronq.], *Arabis drummondii* A. Gray, *Arnica tomentosa* Macoun [*A. alpina* (L.) Olin & Ladau var. *tomentosa* (Macoun) Cronq.], *Carex petricosa* Dewey var. *misandroides* (Fern.) Boivin, *Festuca rubra* L. var. *prolifera* (Piper) Piper *ex* Robinson, *F. saximontana* Rydb., *Gymnocarpium robertianum* (Hoffm.) Newm., *Sphenopholis intermedia* (Rydb.) Rydb. [*S. obtusata* (Michx.) Scribn. var. *major* (Torr.) K. S. Erdman], *Woodsia alpina* (Bolton) S. F. Gray and *W. glabella* R. Br.

Three species, *Androsace septentrionalis, Woodsia alpina,* and *W. glabella* are circumpolar with southern disjunct populations; the latter two occur as far south as New York, Vermont and Maine. Four other species, *Arabis drummondii, Festuca rubra* var. *prolifera, F. saximontana,* and *Sphenopholis intermedia* are essentially transcontinental, with southern stations in United States. *S. intermedia,* for instance, occurs as far south as Arizona, Texas and Florida. *Arnica tomentosa* is a western alpine species represented by disjunct populations in Newfoundland. Several of these rare vascular plants with arctic or cordilleran affinities, such as *Androsace septentrionalis, Arnica tomentosa, Woodsia alpina,* and *W. glabella,* seem to have become isolated from their main distribution areas, according to the geohistorical scenario discussed by authors such as Drury (1969), Morisset (1971), Rousseau (1974), Miller and Thompson (1979) and Marquis (1981). The arctic-alpine species may have preceded glacial movement southward and survived in coastal refugia or periglacial tundra zones. The cordilleran species could have migrated to the eastern part of the continent by a discontinuous tundra corridor at the southern margin of the glacier, as outlined by Rousseau (1953). In the late-glacial period, climatic and edaphic conditions may have been suitable for rapid plant migration (Miller & Thompson, 1979) and widespread colonization by these arctic-alpine elements on such favourable periglacial habitats as raw morainic deposits (Rousseau, 1974). With subsequent climatic change and reinvasion by more competitive boreal flora, disjunct elements may have survived in relict habitats such as alpine summits, cold sea cliffs, and unstable serpentine or limestone rock. On the other hand, Belland (Belland, R. 1981. M. Sc. Thesis, Memorial University, Newfoundland) has evoked the original nunatak theory (Fernald, 1925) of survival in ice-free, alpine refugia as a possible explanation for the presence in Bonne Bay of widely-disjunct, arctic-alpine and cordilleran bryophytes. He cites recent glacial geological evidence by Grant (1977a, b) in support of Wisconsin-age nunataks in the study area.

Four other calcicolous species of these limestone outcrops which occur in eastern North America are *Antennaria cana, A. gaspensis, Carex petricosa* var. *misandroides,* and *Gymnocarpium robertianum (s. str.).* The latter is an amphi-Atlantic species; the three former ones are endemic to eastern Canada. *Carex petricosa* var.

misandroides is restricted to Québec (Gaspé, Mistassini and Arctic) and to Newfoundland (west coast). *Antennaria cana* and *A. gaspensis,* endemics to the Gulf of St. Lawrence area, are found only in southeastern Québec (Gaspé and Anticosti) or in western Newfoundland.

Endemism around the Gulf of St. Lawrence has attracted the attention of botanists since the explorations of Fernald and Marie-Victorin. Although many of the endemic taxa proposed by these authors have been discredited by subsequent systematic work, others have been maintained as credible species or varieties, isolated by intense local selection. These *Antennaria* species illustrate development of distinctive endemic characters, even though their taxonomic status may remain questionable. Authors such as Scoggan (1978–79) have treated them as hardly separable variants, referable to widespread, polymorphic northern species.

Except for *Antennaria cana,* a calcicolous species found on a rich serpentinic site (Ca:Mg ratio 1.1, Bouchard et al., 1985a), the 11 other species are found on limestone cliffs and talus, characterized by rapidly-drained to well-drained soils. The richness of these rare vascular plant communities varies generally according to their stability. For instance, *Festuca rubra* var. *prolifera* was found in a well-stabilized talus community of 38 species dominated by *Juniperus communis* L., whereas *Sphenopholis intermedia* was found on an eroding scree slope with 18 accompanying species. This stability or lack thereof is reflected in the carbon content of the soils; well-stabilized sites have a thick humus developed on the underlying limestone in contrast to less stabilized sites (Bouchard et al., 1985a). On the other hand, a few well-protected and rather stable microhabitats found in the crevices of limestone cliffs are very poor in vascular plants. For example, *Woodsia alpina* and *W. glabella* are found in stands characterized by only three species each. All these communities include numerous other calcicolous species such as *Anemone multifida* Poiret, *A. parviflora* Michx., *Arnica lonchophylla* Greene *ssp. chionopappa* (Fern.) Maguire, *Cypripedium calceolus* L., *Dryas integrifolia* Vahl, *Oxytropis johannensis* (Fern.) Fern. [*O. campestris* (L.) DC. var. *johannensis* Fern.], *Potentilla nivea* L., and *Saxifraga aizoon* Jacq. [*S. paniculata* P. Miller].

Most of the rare plants restricted to limestone colonize constantly disturbed habitats for which they are well adapted. Periodically, a population will be destroyed by a talus landslip while another will establish a foothold as new habitats are created. These natural cycles should maintain the presence of these rare vascular plants in the Park. Future field search may eventually re-discover populations of *Androsace septentrionalis,* not observed since its discovery in 1929 by Fernald and populations of *Carex petricosa* var. *misandroides,* not observed since its discovery in 1958 by Elkington.

Alpine Plateau

In the alpine plateau land region of Gros Morne National Park, there are 15 rare vascular plants. All are found in the tundra barrens biophysiographic unit, which is taken to include special microhabitats such as zones of snow accumulation and sheltered alpine ravines and slopes occurring adjacent to the more extensive, exposed plateau barrens (Bouchard et al., 1978).

Rare species in the alpine flora include *Athyrium distentifolium* Tausch *ex* Opiz var. *americanum* (Butters) Boivin, *Cassiope hypnoides* (L.) D. Don, *Epilobium anagallidifolium* Lam., *Gnaphalium norvegicum* Gunn., *G. supinum* L., *Lycopodium alpinum* L., *Oxyria digyna* (L.) Hill, *Poa fernaldiana* Nannf., *Salix herbacea* L., *Saxifraga rivularis* L., *S. stellaris* L. var. *comosa* Poiret [*S. foliolosa* R. Br. var. *foliolosa*], *Sibbaldia procumbens* L., *Thelypteris limbosperma* (All.) H. P. Fuchs, *Vahlodea atropurpurea* (Wahlenb.) Fries [*Deschampsia atropurpurea* (Wahlenb.) Scheele] and *Viola palustris* L. Most of these species belong to the arctic-alpine floristic element, characterized by widespread, arctic-circumpolar distributions whose ranges extend southward in the eastern part of the continent to isolated or disjunct alpine habitats such as occur in the Long Range Mountains of western Newfoundland, on the alpine summits of the Shickshocks on the Gaspé Peninsula and on the alpine peaks of New England. Ten of these species, including *Cassiope hypnoides, Epilobium anagallidifolium, Lycopodium alpinum, Oxyria digyna, Salix herbacea, Saxifraga rivularis, S. stellaris* var. *comosa, Sibbaldia procumbens, Thelypteris limbosperma* and *Viola palustris* typically share this general distribution pattern. *Thelypteris limbosperma* is an exceptional case, in that it shows a striking east/west disjunction for North America, in an otherwise undisrupted circumpolar distribution. The only known colony of this species, which is isolated in the large gap between western North America and Europe, was discovered in Gros Morne National Park and has been the subject of previous papers by Bouchard and Hay (1976a) and Bouchard et al. (1977).

Three of the rare plants of this biophysiographic unit, *Gnaphalium norvegicum, G. supinum* and *Vahlodea atropurpurea,* have boreal to arctic amphi-Atlantic ranges bridging northeastern North America and northwestern Europe.

Athyrium distentifolium var. *americanum* is an essentially western alpine fern with a few, highly disjunct, rare populations in the Gulf of St. Lawrence region.

Only one rare endemic, *Poa fernaldiana,* is confined to the tundra barrens unit of the upland plateau region. This distinctive grass is rare throughout its restricted range on alpine summits in the Gulf of St. Lawrence region and New England.

The isolated occurrence of this arctic or cordilleran flora in disjunct, alpine outposts of eastern North America has been discussed in connection with similar elements which occur as disjunct populations on the limestone escarpments in the park. An alternative hypothesis, that of long-distance dispersal to disjunct eastern stations, cannot be disregarded for the mainly cordilleran ferns *Athyrium distentifolium* var. *americanum* and *Thelypteris limbosperma* (Bouchard et al., 1977). Wagner and Rouleau (1984) suggested this same possibility for another rare cordilleran fern in Newfoundland, *Polystichum* × *scopulinum* D. C. Eaton.

All of the 15 rare species studied in this biophysiographic unit have been recorded from snowbed zones (zabois) or more sheltered alpine ravines and slopes, which contrast strikingly with the exposed tundra vegetation on the adjoining plateau barrens. Damman (1983) emphasized that species such as *Cassiope hypnoides, Oxyria digyna* and *Salix herbacea* are restricted to the snowbeds of the Northern Long Range and similar sites in the Serpentine Range of the Western Newfoundland Ecoregion. The cool, seepy conditions of these habitats favour richer herbmat communities often dominated by many sub-alpine species such as *Clintonia borealis* (Ait.) Raf., *Coptis groenlandica* (Oeder) Fern. [*C. trifolia* (L.) Salisb. ssp. *groenlandica* (Oeder) Hultén], *Cornus canadensis* L., *Deschampsia flexuosa* (L.), Trin., *Dryopteris spinulosa* (O. F. Muell.) Watt and *Solidago macrophylla* Pursh. More characteristic of these sites is the arctic-alpine flora composed of relatively abundant species such as *Carex bigelowii* Torr., *C. stylosa* C. A. Meyer, *Diapensia lapponica* L., *Juncus trifidus* L., *Loiseleuria procumbens* (L.) *Desv. and Phyllodoce caerulea* (L.) Bab., which often grade into these sites from the exposed tundra on the adjoining plateau barrens. Except for the *Cassiope hypnoides* colony found on the gabbro talus, the soils sampled are relatively acidic with moderately decomposed organic accumulation (Bouchard et al., 1985a).

Belland (1983) has reported similar findings for the widely-disjunct bryophyte flora which is also restricted to the alpine snowbed communities in Gros Morne. The special ecological conditions created in these micro-habitats due to accumulation of late-lying snow and a significantly shorter growing season have been studied in comparable situations in northern Québec (Filion & Payette, 1982) and on the Gaspé Peninsula (Boudreau, F. 1981. M. Sc. Thesis, Université Laval, Québec). The rare arctic-alpine plants are well adapted to this micro-environment and they may illustrate a relict flora which has persisted since the late-glacial period.

Unquestionably, the highland plateau region of the Park remains relatively unexplored botanically, a fact which may explain the concentration of apparently rare species based on what we presently known of the flora. Two rare species included here, *Lycopodium alpinum* and *Thelypteris limbosperma,* were new additions to the flora of Newfoundland (Bouchard & Hay, 1974, 1976a; Bouchard et al., 1977). Two other remarkable arctic-alpine plants, *Saxifraga stellaris* var. *comosa* and *S. rivularis,* are newly reported for St. Barbe South District, previous records being known only from the tip of the Northern Peninsula. Finally, another three species, *Athyrium distentifolium* var. *americanum, Epilobium anagallidifolium* and *Poa fernaldiana* constitute new records for the Gros Morne National Park area of St. Barbe South District. With further exploration, perhaps other arctic-alpine species will be added to the flora of the Park. [René Belland found an additional rare plant, *Ranunculus pedatifidus* Sm., in an alpine ravine on Gros Morne Mountain, 27 August 1984 (substantiating specimen deposited at NFLD, pers. comm., 24 January 1985).] By the same token, some of the species presently considered to be rare may prove to be more frequent throughout the alpine plateau region.

Serpentine Tableland

The Tableland is treated as a distinct land region comprising one biophysiographic unit (Bouchard et al., 1978, 1985b), including the altered gabbro outcrops and talus of the mafic highland which intergrade with the serpentine massif.

The five rare vascular plants of the Tableland are *Arenaria marcescens* Fern. [*Minuartia marcescens* (Fern.) House], *Danthonia intermedia* Vasey, *Eleocharis nitida* Fern., *Festuca altaica* Trin. *in* Ledeb. and *Salix arctica* Pallas. Three of these, *Danthonia intermedia, Eleocharis nitida,* and *Festuca altaica,* are mostly boreal species occurring transcontinentally in widely-scattered, isolated localities. Populations of the two grasses become more frequent towards the western part of their range, whereas *Eleocharis nitida* is more widely represented in the east. *Salix arctica* has a continuous circumpolar distribution with isolated populations occurring southward, in the eastern part of the continent, on the serpentine massifs of western Newfoundland and on the Gaspé Peninsula. *Arenaria marcescens* is an endemic taxon of northeastern North America. It is rare throughout its restricted range, being confined to serpentine exposures of western Newfoundland, the Gaspé Peninsula and Vermont. It is perhaps better interpreted as a disjunct variety of cordilleran affinity to the western species *A. obtusiloba* (Rydb.) Fern. [*Minuartia obtusiloba* (Rydb.) House].

Of these rare species, only *Arenaria marcescens* is found exclusively on serpentine substrate. *Salix arctica,* although restricted to this habitat in the Gulf of St. Lawrence, is not strictly serpentinicolous elsewhere in its range. Similarly, although they are known chiefly from this area in the Park, the other three species may colonize different types of rocky or peaty barren.

Arenaria marcescens is a frequent component of the sparse vegetation colonizing open rock and gravel polygon barrens. Characteristic species recorded from the sample stand include *Armeria maritima* (P. Miller) Willd. ssp. *labradorica* (Wallr.) Hultén, *Carex scirpoidea* Michx., *Rhododendron lapponicum* (L.) Wahlenb., *Salix glauca* L., *Senecio pauperculus* Michx. and *Silene acaulis* (L.) Jacq. (Bouchard et al., 1985a). The rare *Danthonia intermedia* and *Festuca altaica* are found on screes and talus in the protective cover of dense, stunted scrub communities dominated by tolerant woody species such as *Juniperus communis, J. horizontalis* Moench, *Larix laricina* (Du Roi) K. Koch and *Potentilla fruticosa.* The sample population of *Eleocharis nitida* was found in an open, gravelly seep on a serpentine moraine at the base of the Tableland. The Mg concentration and the Ca:Mg ratio (Bouchard et al., 1985a) of sampled sites for four of the rare species is consistent with those reported for serpentine soil throughout the world (Proctor & Woodwell, 1975). Although *Salix arctica* was collected in 1973 and

1978, we were unable to re-locate stands of this rare willow in 1984.

The five rare species are well established in a diversity of habitats unique to the Tableland. The sparse vegetation of these barren wastelands and their unique ecology have been discussed for Gros Morne National Park by Bouchard et al. (1978) and Dearden (1979). Because of the restrictive ecological factors, the serpentine flora, including the rare species, is highly adapted to this particular environment. *Arenaria marcescens* is quite common on the Tableland, but populations of the four other species are few in number.

The cordilleran fern. *Adiantum pedatum* L. ssp. *calderi* Cody [*A. pedatum* var. *aleuticum* Rupr.], although restricted to serpentine in Newfoundland, is fairly widespread and frequent in its habitat and was not treated as rare in the Park. It may still warrant consideration in a forthcoming study of Newfoundland's rare plants.

ORDINATION OF RARE PLANT STANDS

To present an overview of the rare plant communities and to clarify their relationships to abiotic variables, a principal coordinate ordination of the data (Bouchard et al., 1985a, and CISTI) was performed (Figure 3). Five groups are easily identified: the coastal plain land region comprising the tidal flats and brackish shores; the coastal plain peatlands; the limestone escarpments land region; the alpine plateau land region; and the serpentine tableland land region. Three abiotic variables are correlated with the first axis: pH $-.5483$ ($p < .001$); Mg $-.4144$ ($p < .01$); altitude .6185 ($p < .001$) and four with the second axis: cation exchange capacity .4767 ($p < .05$); Mg .5043 ($p < .05$); Na .4698 ($p < .05$); drainage .6350 ($p < .001$).

On the first axis, soil pH and altitude are important abiotic variables. The oligotrophic sites are on the right, especially associated with the alpine plateau land region, while the more eutrophic sites are on the left with the limestone escarpment land region and the serpentine tableland land region. The rare plant stands on peatlands occupy an intermediate position because they are not found on oligotrophic peats, which are abundant in the Park, but are confined to restricted eutrophic sites (fens). The tidal flat stands fall in the center of the ordination because they share few species with the other plant communities. On the right are found the high altitude arctic-alpine plant communities. Altitude is also an important factor contributing to the presence of rare plants in the limestone escarpments land region. Within this land region, the four stands on the

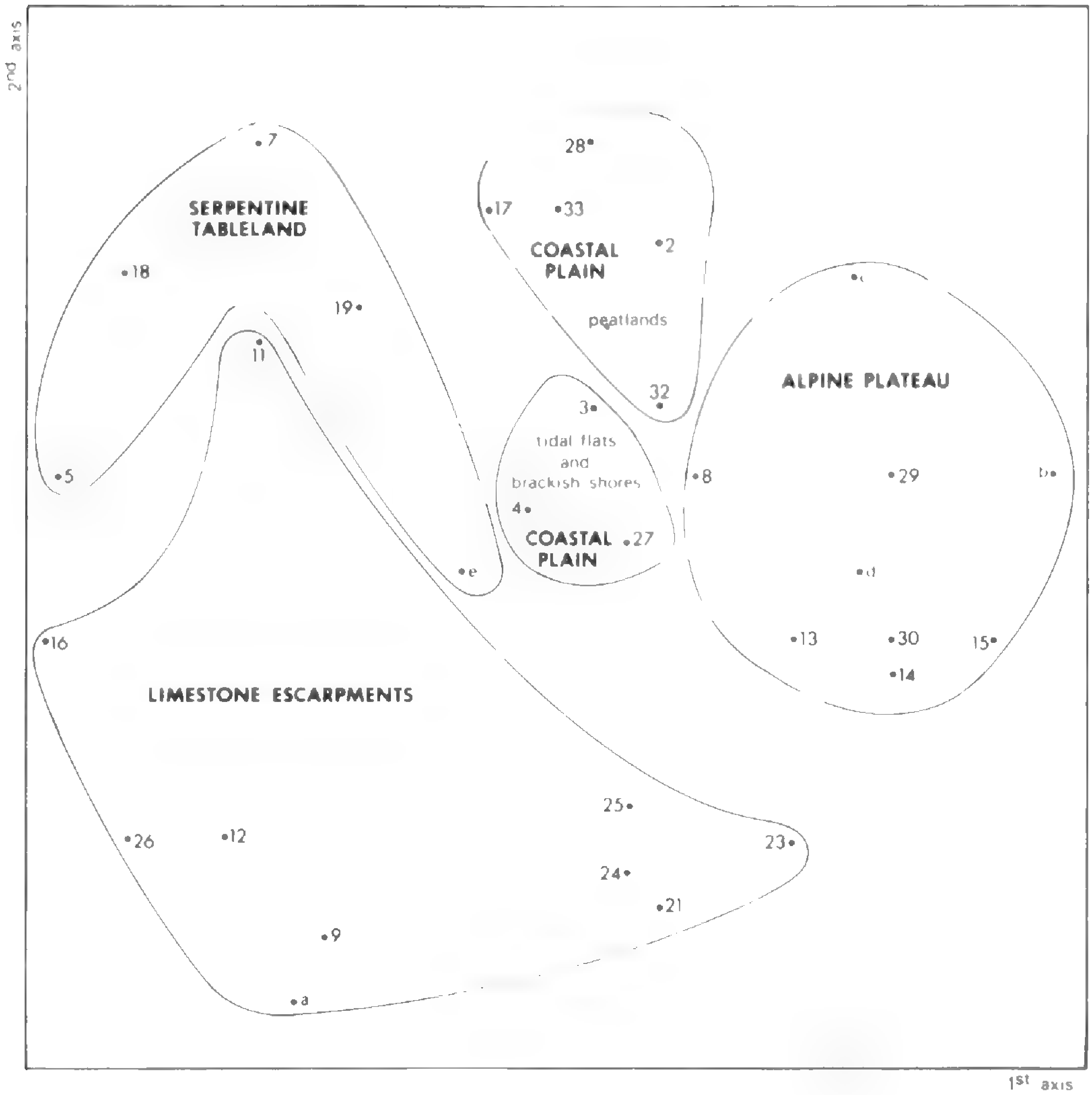

Figure 3. Principal coordinate ordination and biophysiographic affinities for the rare plant communities. Stand numbers refer to sample populations based on data in Bouchard et al. (1985a, and CISTI).

right (21, 23, 24 and 25) are all situated at an elevation higher than 600 m while the other stands are usually at an elevation of less than 100 m (Bouchard et al., 1985a).

On the second axis, drainage is an important abiotic variable. The rare plant stands on limestone, characterized by rapidly-drained to well-drained soils, fall in the lower part of the ordination, while the stands on very poorly-drained, organic soils are in the middle and upper part. These organic soils are also characterized by a higher cation exchange capacity. The magnesium content of the serpentine soils accounts for the segregation of the Tableland stands from those of the limestone escarpments land region. Some integration exists between stands on these latter basic substrates because these open unstable habitats, characterized by their low plant cover, are colonized by many of the same pioneer species.

The ordination graphically illustrates a clear segregation of rare plant colonies of Gros Morne National Park according to community composition and important abiotic variables. Occurrence of many of the exceptional species in the Park can be directly attributed to the presence of special restricted habitats which are reflected in the ordination.

CONCLUSION

Gros Morne National Park has an important heritage of rare vascular plants. We have treated as rare 43 taxa among a total vascular flora of about 700 species. Despite the somewhat subjective nature of what constitutes rarity, these taxa are considered to be the most significant examples because they are species which are rare not only within the Park territory, but they have very few known populations in Atlantic Canada.

Rare plants owe their status to a complex variety of interrelated geohistorical, genetic and ecological factors (Brouillet, 1985; Drury, 1980; Stebbins, 1980). In Gros Morne National Park, they are for the most part restricted to special, localized habitats such as tidal flats, limestone escarpments or talus, serpentine barrens, eutrophic peaty areas and alpine snowbeds. Stebbins (1980) described this concept as "ecological islands" of isolated or marginal populations of rare species established and persisting on special, restricted habitats.

The primary importance of these rare plants lies in the complex biogeographic problems and interpretations which they pose. For example, *Antennaria gaspensis, Arenaria marcescens* and *Poa fernaldiana* are rare endemics of northeastern North America. The isolated populations of *Arnica tomentosa, Athyrium distentifolium* var. *americanum* and *Thelypteris limbosperma* show remarkable eastern disjunctions from their main range of distribution in the western part of the continent. The arctic-alpine species *Salix herbacea, Saxifraga rivularis* and *Sibbaldia procumbens* occur isolated far to the south of their arctic-circumpolar ranges on a few alpine summits such as the Long Range Mountains. The peripheral populations of *Elymus virginicus* and *Solidago sempervirens,* occurring at the northern limit of their native range, appear to be rare in Newfoundland. Finally, a few species such as *Danthonia intermedia, Drosera linearis* and *Eriophorum gracile,* though widely dispersed continentally, are rare in Newfoundland and several other provinces or states.

The only practical means of protecting these rare plant populations is to preserve the special habitats where they occur. Except for *Arenaria marcescens,* which is relatively common on the serpentine barrens, few populations of these rare species are known in the Park. Some extreme cases such as *Androsace septentrionalis, Carex misandroides* var. *petricosa, Eriophorum gracile* and *Thelypteris limbosperma* are known from only one population, and some have not been reobserved for many years. Fragile habitats such as the limestone cliffs or talus and the alpine snowbeds must receive particular attention if they are to be preserved.

Bratton and White (1981) discussed the problems involved in management of rare or endangered plant populations after the initial steps have been taken to establish a preserve. For Gros Morne National Park, a management or monitoring program of the populations seems neither necessary nor advisable because of the remoteness of the rare plant colonies. Attempts at management could in fact be more detrimental than beneficial, especially where the habitats are particularly fragile. The authorities should, however, protect the sites and show prudence about revealing their exact locations. Nevertheless, they should facilitate population studies such as that done on *Cypridepium passerinum* Rich., in Pukaskwa National Park (Keddy et al., 1983).

The intrinsic appeal of rare plants should not be overplayed by the nature interpretation program of the Park. With the exception of the Showy Lady's-slipper, the rare plants of Gros Morne offer little visual appeal to all but the most ardent botanist. Rather, the accent should be placed on the fascinating geohistorical explanations for the establishment and persistence of these species, and the biogeographical problems raised by the persence of such a diversity of endemic, peripheral and disjunct elements in the Park's vascular flora.

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A. B.
JARDIN BOTANIQUE DE LA VILLE DE MONTRÉAL
4101 EST, RUE SHERBROOKE
MONTRÉAL (QUÉBEC) CANADA H1X 2B2

A. B., S. H.
INSTITUT BOTANIQUE DE L'UNIVERSITÉ DE MONTRÉAL
4101 EST, RUE SHERBROOKE
MONTRÉAL (QUÉBEC) CANADA H1X 2B2

C. G.
CENTRE DE RECHERCHES ÉCOLOGIQUES DE MONTRÉAL
UNIVERSITÉ DE MONTRÉAL
5858 CHEMIN CÔTE-DES-NEIGES, BUREAU 400
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Y. B.
DÉPARTEMENT DE SCIENCES BIOLOGIQUES
UNIVERSITÉ DU QUÉBEC À MONTRÉAL, C. P. 8888, SUCC. A,
MONTRÉAL (QUÉBEC) CANADA H3C 3P8

NEW MESOAMERICAN SPECIES OF *CYPERUS* (CYPERACEAE)[1]

GORDON C. TUCKER

ABSTRACT

Four species of the genus *Cyperus* are described, illustrated, and compared to their nearest relatives. These are: *C. matudae* and *C. breedlovei* (Subgenus *Protocyperus*) from the Pacific slope of Chiapas, Mexico; and *C. wilburii* and *C. svensonii* (Subgenus *Cyperus*) from the lowlands of the Isthmus of Tehuantepec, and from the uplands of Chiapas, Guatemala, Honduras, and Nicaragua, respectively.

Key Words: Cyperaceae, *Cyperus*, new species, Mexico, Central America

Four new species of *Cyperus* have been detected in a study of the genus in Mexico (Tucker, G. C. 1985. Unpubl. Ph. D. thesis, Duke University, Durham, N. C.). These new species are members of the two largest subgenera of *Cyperus:* subgenus *Protocyperus* K. A. Lye, in which the plants have trigonous achenes, digitate clusters of spikelets, and eucyperoid (non-Kranz) anatomy (Lye, 1981); and subgenus *Cyperus,* in which the plants have trigonous achenes, spicate inflorescences, and chlorocyperoid (Kranz) anatomy (Raynal, 1973). A detailed account of the characteristics of the subgenera appeared in Kükenthal (1935–36) and Tucker (1983).

Cyperus matudae G. C. Tucker *sp. nov.* TYPE: MEXICO. Chiapas, Mt. Ovando, pine land, 1250–2370 m, July 1938, *Matuda 2553* (HOLOTYPE: MICH; ISOTYPES: F, GH, LL, NY). (Figure 1).

Plantae perennes, 50–75 cm alta. Culmi triquetri, scabri in angulis, 1.3–2.5 mm crassi. Bracteae 6–8, 3–30 cm longae, 2–10 mm latae. Radii 10 vel 11, ad 15 cm longi; radii secundarii ad 4 cm longi; radii tertiarii ad 15 mm longi. Spiculae digitatae, lineari-lanceolatae, compressae, 7–15 mm longae, 2.3–3.5 mm latae. Squamae deciduae, oblongo-ellipticae, 2.2–2.4 mm longae, cuspidae apicali 0.4–0.8 mm longo. Stamina tria. Stigmata tria. Achenia trigona, ellipsoidea, 1.8–2.0 mm longa, circa 1.2 mm lata. *Cypero chorisantho* C. B. Clarke affinis.

Perennials, 50–75 cm tall. Rhizomes horizontal, indurate, clothed

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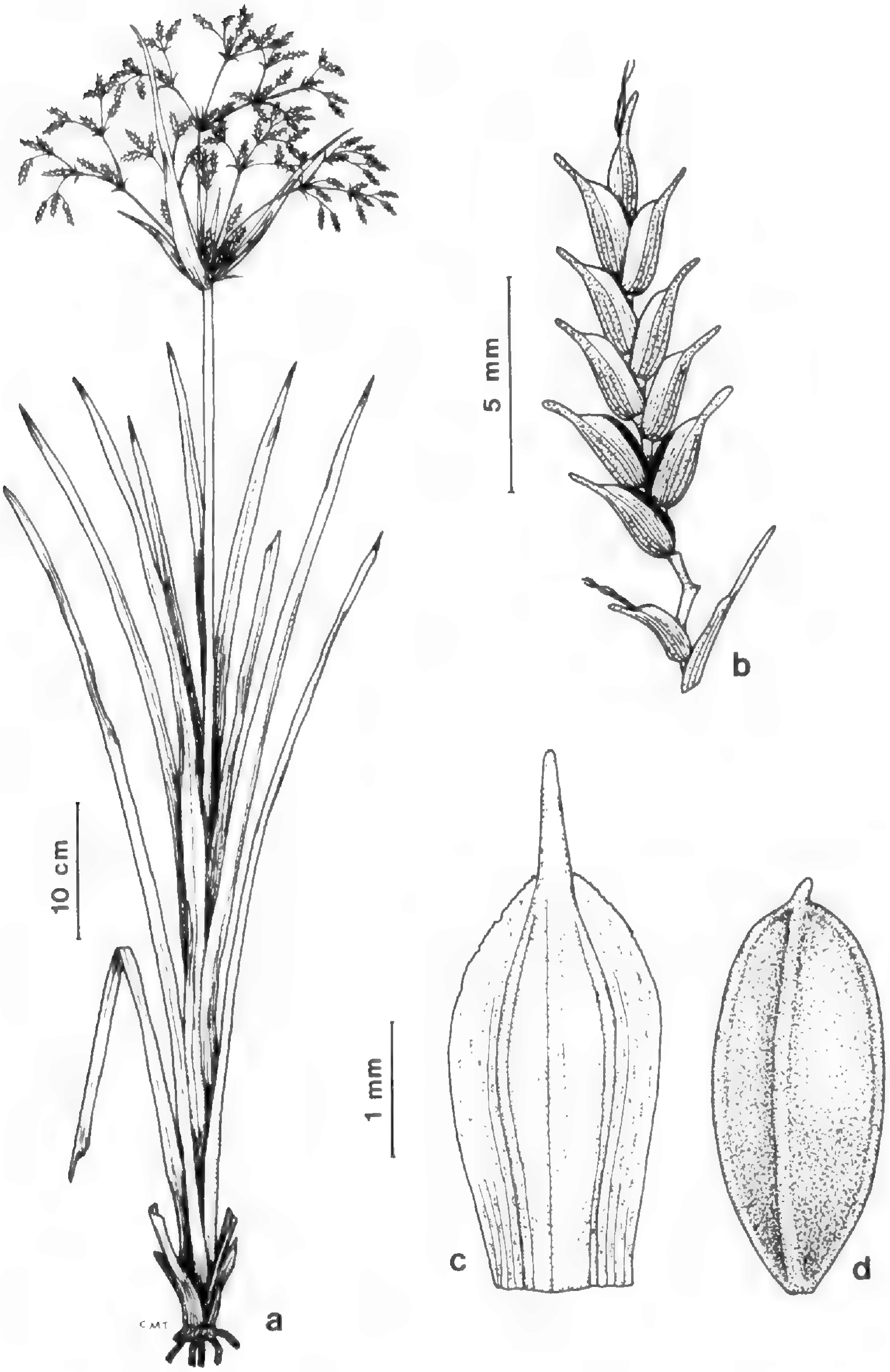

Figure 1. *Cyperus matudae*. **a**. plant; **b**. spikelet; **c**. scale (abaxial view); **d**. achene.

with fibrous leaf bases. Culms triquetrous, scabrous on the angles only, especially above, 1.3–2.5 mm thick. Leaves flat to subtly plicate, about as long as the culm, 5–15 mm wide, the margins and keels scabrellate. Inflorescence bracts 6–8, 3–30 cm long, 2–10 mm wide, vertical to ascendent at (60) 75°. Rays 10–11, up to 15 cm long; secondary rays 3–8 per primary ray, 10–40 mm long; tertiary rays 3–15 mm long. Spikelets digitate in groups of 1–3, linear-lanceolate, 7–15 mm long, 2.3–3.5 mm wide (including the apices of the scales), greenish brown, deciduous at maturity; rachilla slightly flexuous, wingless, persistent. Scales 8–16, oblong-elliptic, 2.2–2.4 mm long (the excurved cusp 0.4–0.8 mm long), 1.4–1.6 mm wide, laterally 3–4 nerved, reddish to brownish green, medially 3–7 nerved, the midvein green, smooth or scabrellate distally. Stamens 3; anthers 0.9–1.2 mm long, the setose apices of the connectives an additional 0.1–0.2 mm long. Styles 0.6–0.8 mm long; stigmas 3, (1.2) 1.6–2.6 mm long. Achenes trigonous, ellipsoid, 1.8–2.0 mm long, about 1.2 mm wide, sessile, apiculate, papillose, brown.

Endemic to southern Chiapas, Mexico, *Cyperus matudae* is known from only two collections made near the Guatemalan border. Plants with mature achenes have been collected in July and August. *Cyperus matudae* is placed in subgenus *Protocyperus* K. A. Lye, because of its trigonous achenes and digitately arranged spikelets. Both known collections of this new species had been identified previously as "*C. diffusus* Vahl" [= *C. laxus* Lam.], a widespread neotropical species (Tucker, 1983). *Cyperus matudae* differs strikingly from *C. laxus* in features of the achenes and scales, and in its more highly branched inflorescences. *Cyperus laxus* has only primary and secondary rays, while all available specimens of *C. matudae* have tertiary rays as well. This species is named for Professor Eizi Matuda (1894–1978), specialist on the flora of Mexico, who made both known collections of this species.

ADDITIONAL SPECIMEN: **Mexico.** Chiapas, Escuintla, Finca Fuárez, 12 Aug. 1937, *Matuda 1937* (GH, MICH).

Cyperus breedlovei G. C. Tucker *sp. nov.* TYPE: MEXICO. Chiapas, on Hwy. 211 about 25 km N of Huixtla, in crevices on rocky roadcut in forest with *Bursera,* 700 m, 28 July 1984, *Tucker & Schwartz 2686* (HOLOTYPE: DUKE; ISOTYPES: BH, CAS, ENCB, F, GH, K, MEXU, MICH, MO, NY, US, WIS). (Figure 2).

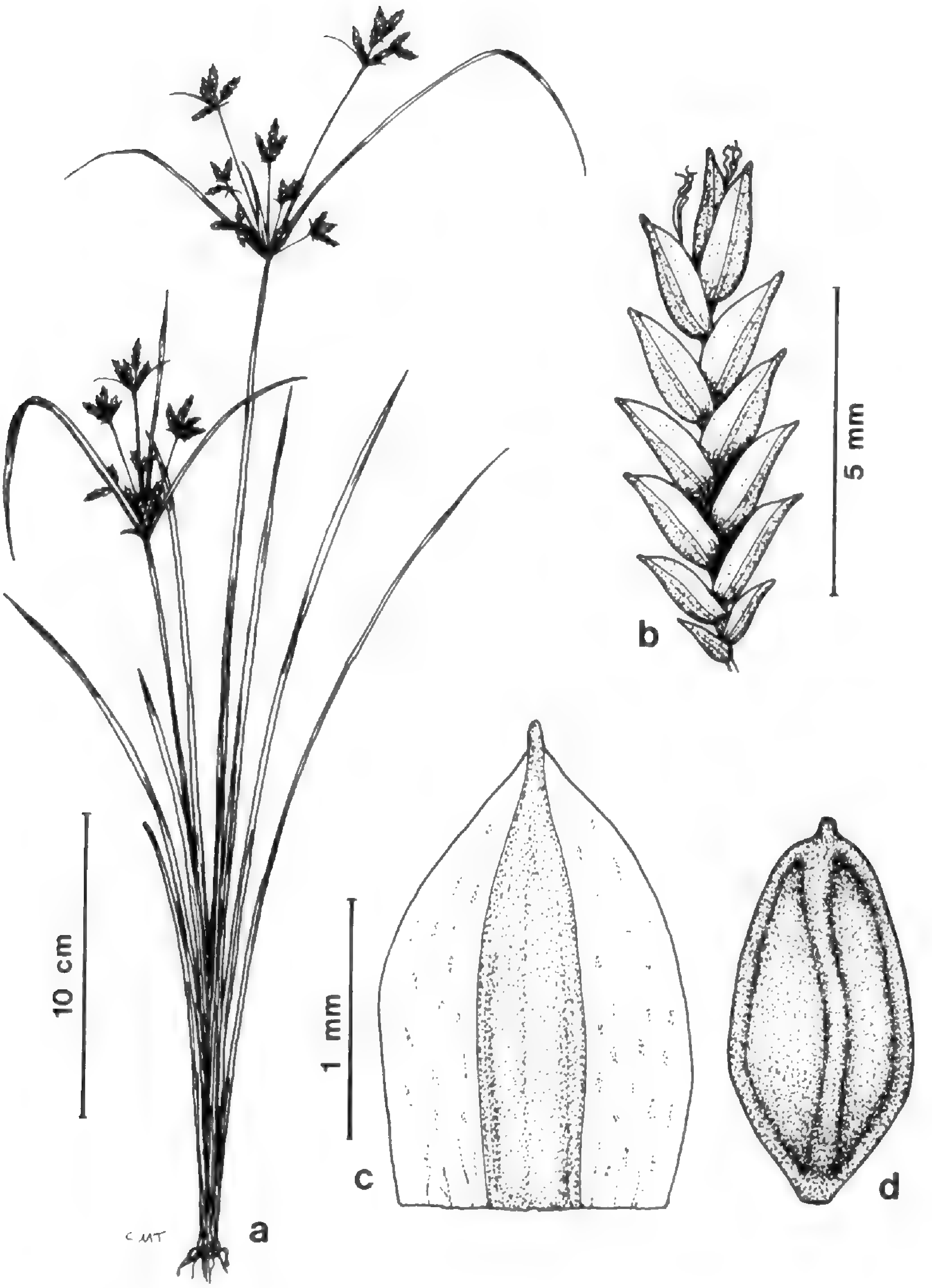

Figure 2. *Cyperus breedlovei*. **a.** plant; **b.** spikelet; **c.** scale (abaxial view); **d** achene.

Plantae perennes, 25–50 cm alta. Bracteae 3–5, ad 12 cm longae; bractea longissima erecta vel valde adscendens. Spiculae digitatae, 1–5 (7), lineari-oblongae, 4–15 mm longae, 1.8–2.4 mm latae.

Squamae oblongo-lanceolatae, mucrone apicali 0.2–0.4 mm longo. Stamina tria. Stigmata tria. Achenia trigona, ellipsoidea, 1.2–1.4 mm longa, usualiter 0.6 mm lata. *Cypero chalarantho* Presl affinis.

Perennials, 25–50 cm tall. Rhizomes indurate, about 2 mm thick. Culms solitary or 2–3 together, trigonous and smooth below, triquetrous and scabrellate (or smooth) above, 0.8–1.2 mm thick. Leaves 1–5, conduplicate, 10–40 cm long, 2–3.5 mm wide, the margins and keels scabrellate. Inflorescence bracts 3–5, up to 12 cm long, 1–2.5 mm wide, the margins and keels scabrellate, the longest erect or strongly ascendent (appearing as a continuation of the culm). Rays 2–8, up to 4 cm long, scabrellate; secondary rays absent or 1–4, up to 1 cm long. Spikelets digitate, 1–5 (7), linear-oblong, compressed, reddish brown, 4–15 mm long, 1.8–2.4 mm wide; rachilla straight, wingless, persistent. Scales 7–16, oblong-lanceolate, 1.8–2.3 mm long (including the mucronate apex of 0.2–0.4 mm), 1–1.2 mm wide, laterally reddish brown, 2–3 nerved, the margins sometimes sparsely ciliate-scabrellate, medially green, 3–5 nerved, the midvein scabrellate, deciduous. Stamens 3; anthers about 1 mm long, the setose connective apices about 0.2 mm long. Styles 0.2–0.4 (0.6) mm long; stigmas 3, 2.3–2.5 mm long. Achenes trigonous, ellipsoid, 1.2–1.4 mm long, about 0.6 mm wide, apiculate, cuneate to substipitate, puncticulate, brown.

Endemic to southern Chiapas, *Cyperus breedlovei* is known from only three collections from the type locality: crevices in steep moist ledges in tropical forest at about 700 m elevation. Flowering and fruiting collections have been made in July and October. *Cyperus breedlovei* is distinguished from all other Mexican and Central American species of subgenus *Protocyperus* by the combination of linear-oblong spikelets, reddish brown mucronate scales, and ellipsoid apiculate achenes. The oblong-lanceolate scales nerved nearly to the margins, the straight mucronate apices of the scales, and the ellipsoid achenes indicate that the new species is most closely related to *C. chalaranthus* Presl of northwestern South America (Tucker, 1983). *Cyperus breedlovei* differs from *C. chalaranthus* in having the longest inflorescence bract erect to ascendent (at 60°), and the scales reddish brown and scabrellate along the midvein; in *C. chalaranthus* the bracts are horizontal to ascendent (at 30°) and the scales light green and smooth. This species is named for Dennis E. Breedlove, diligent investigator and collector of the flora of Chiapas, who gathered the first collection.

ADDITIONAL SPECIMENS: **Mexico.** CHIAPAS: Mpio. Motozintla, 25–27 km NE of Huixtla on the road to Motozintla [Hwy. 211], 7 Oct. 1972, *Breedlove 28603* (DS); 15 miles N of Huixtla on Rte. 211, 28 July 1984, *Wilbur 35843* (DUKE).

Cyperus wilburii G. C. Tucker *sp. nov.* TYPE: MEXICO. Oaxaca, 8.5 km W of Niltepec on Hwy. 200 at the turnoff to Cerro Iguana, 31 July 1984, *Tucker 2756* (HOLOTYPE: DUKE; ISOTYPES: BH, C, CAS, ENCB, F, GH, K, MICH, MO, NY, US). (Figure 3).

Plantae annuae caespitosae, (5) 10–25 (30) cm alta. Radii simplices; spicae subdigitatae. Spiculae compressae, (3.5) 5–6.5 (7) mm latae, stramineae vel fulvae. Squamae (3.8) 4–4.6 mm longae, (2.4) 2.6–3.2 (3.6) mm latae, cuspide apicali (1.1) 1.3–1.5 (1.6) mm longa. Achenia obovoidea, stipitata, trigona, apiculata, 1.7–2.2 mm longa, 1–1.4 mm lata. *Cypero compresso* L. affinis.

Caespitose annuals, (5) 10–25 (30) cm tall. Roots fibrous, rhizome none. Culms trigonous, smooth, 0.5–1.5 mm thick. Leaves (1) 3–4, (1) 12–20 (30) cm long, 0.5–3 mm wide, conduplicate, the margins and keels scabrellate distally. Inflorescence bracts (2) 3–5 (6), (2) 8–15 (25) cm long, 0.5–4 mm wide, the margins and keels scabrellate, ascendent at 45–60° (the longest bract in some plants erect, looking like a continuation of the culm). Rays 1–3 (5), unbranched, smooth, 1.5–5 cm long, occasionally lacking, the inflorescence in such plants a loose cluster of 3–6 spikelets; rachis smooth, 1.5–3.5 (6) mm long. Spikelets (1) 3–7 (10), oblong to oblong-lanceolate, strongly compressed, (10) 14–20 (32) mm long, (3.5) 5–6.5 (7) mm wide, stramineous to tawny brown; rachilla slightly geniculate, brown to reddish brown, persistent, 0.5–0.8 mm wide, 0.2–0.3 mm thick, the hyaline wings 0.1 (–0.2) mm wide, successive scale scars 2–2.4 (2.6) mm apart on the same side. Scales 10–16 (30), ovate-oblong, (3.8) 4–4.6 mm long, (2.4) 2.6–3.2 (3.6) mm wide, the cusp straight to slightly excurved (1.1) 1.3–1.5 (1.6) mm long, the medial part of the scale greenish, smooth, weakly 3–5 nerved, laterally stramineous to reddish brown, conspicuously 2-nerved midway between the center and margins, deciduous. Stamens 3; filaments 4–5 mm long; anthers oblong, 0.8–0.9 mm long, the connective apices minute. Styles 2–2.5 mm long; stigmas 3, about 0.6 mm long. Achenes trigonous, obovoid, stipitate, 1.7–2.2 mm long, 1.0–1.4 mm wide, apiculate, the base 0.3–0.4 mm long and about as wide, the angles acute, the faces concave, puncticulate, brownish.

Endemic to Mexico, *Cyperus wilburii* occurs in the Pacific Coastal lowlands of the Isthmus of Tehuantepec in the State of Oaxaca.

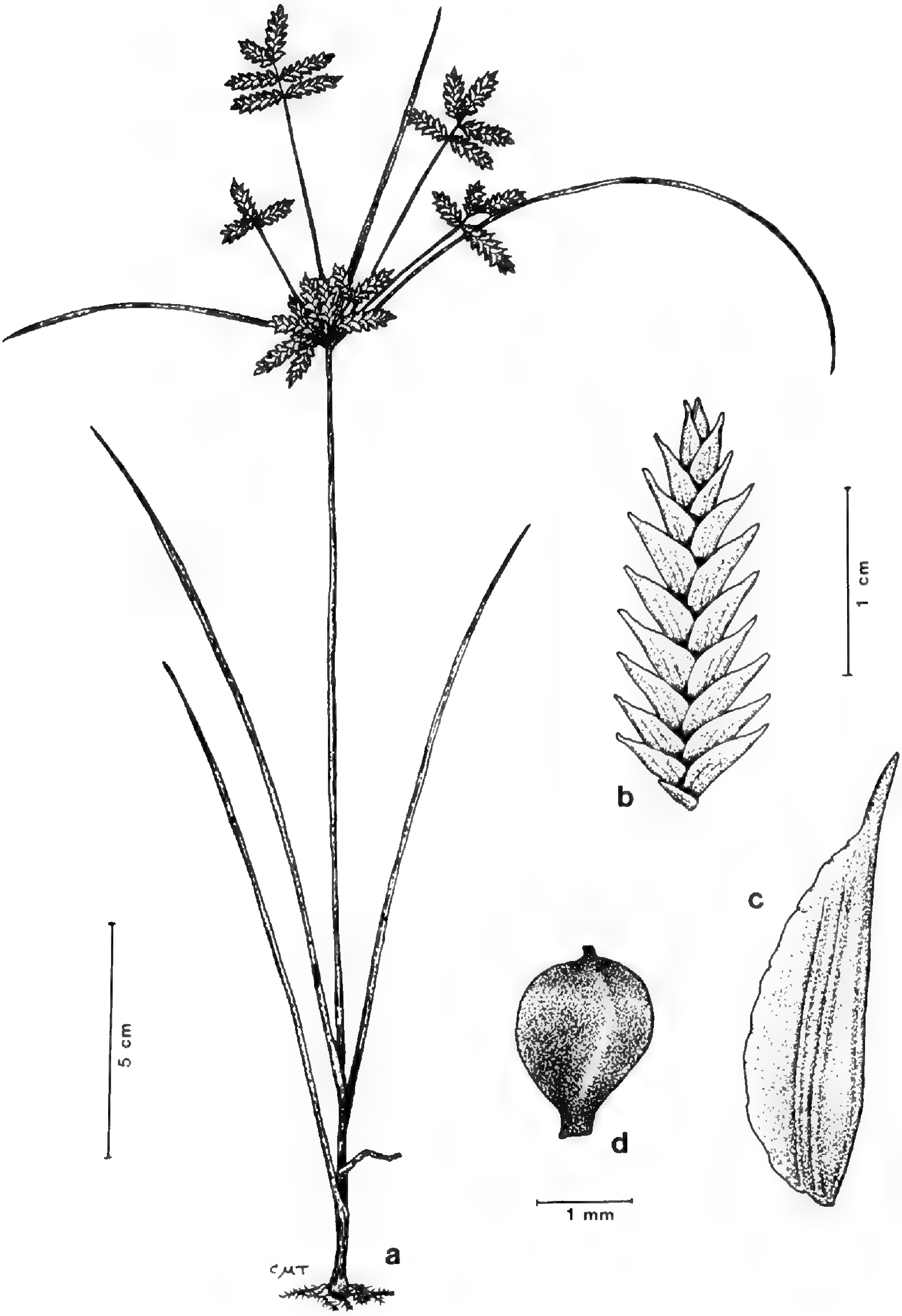

Figure 3. *Cyperus wilburii.* **a.** plant; **b.** spikelet; **c.** scale (abaxial view); **d.** achene.

Apparently uncommon and known from only five collections, it grows in disturbed open soil among thorny shrubs and cacti and in pastured thorn savannas from sea level to about 100 m. A single flowering collection has been made in June; collections made from July through October have mature achenes.

Cyperus wilburii is classified in subgenus *Cyperus*, as indicated by its trigonous achenes and spicate inflorescences. It is closely related to the pantropical and warm temperate *C. compressus* L., as clearly indicated by its annual habit, loosely clustered spikelets, cuspidate scales, and trigonous obovoid achenes. To the unaided eye, *C. wilburii* is easily distinguished from *C. compressus* by its wide (5.0–6.5 mm), stramineous to tawny spikelets; in *C. compressus* the spikelets are only 2.0–3.0 (3.6) mm wide and greenish white. In addition, the achenes of *C. wilburii* are stipitate and larger (1.7–2.2 mm long, 1–1.4 mm wide) than the sessile achenes of *C. compressus* (1–1.5 mm long, 0.9–1.1 mm wide). This new species is named for Robert L. Wilbur, Professor of Botany at Duke University.

ADDITIONAL SPECIMENS: **Mexico.** OAXACA: Ixtepec, 200 ft., 17 Aug. 1935, *Fisher 35258* (ARIZ, F, MO, NY, SMU, TEX, US); along the hwy. to Tehuantepec, 6 km N of Salina Cruz, 30 June 1958, *King 917* (MICH, TEX, US); San Gerónimo, 5 Oct. 1933, *Mell 2115* (NY, US); Route 200, about 5.3 miles W of Niltepec near turnoff to Cerro Iguana, *Wilbur 35922* (DUKE, ENCB).

Cyperus svensonii G. C. Tucker *sp. nov.* TYPE: MEXICO. Chiapas, just E of Colonia Aztlán on Hwy. 195 about 1.7 km N of the Pan American Hwy., along gully in cornfield at about 1000 m, 24 July 1984, *Tucker 2661* (HOLOTYPE: DUKE; ISOTYPES: CAS, ENCB, F, GH, K, MEXU, MICH, MO, NY, US, WIS.) (Figure 4).

Plantae perennes, caespitosae. Culmi trigoni, laevi. Bracteae horizontales vel reflexae. Spicae sessiles, dense cylindricae, albidae. Spiculae ellipsoideae vel oblongo-ellipsoideae, deciduae; rachillae alatae. Squamae obovatae. Achenia trigona, oblongo-ellipsoidea usque ellipsoidea, brunnea usque rubro-brunnea. *Cypero regiomontano* Britt. affinis.

Perennials, 15–55 cm tall. Rhizomes indurate. Culms loosely cespitose, trigonous, smooth, 1–2 mm thick. Leaves 3–9, plicate, 10–35 cm long, 2.5–4 mm wide, the margins and veins scabrous. Inflorescence bracts (3) 4–6, horizontal to reflexed downward parallel to the culm, 3–15 (25) cm long, 1–5 mm wide, the margins and veins scabrous. Inflorescence composed of (2) 4–5 (8) oblong-ellipsoid to oblong-ovoid, densely cylindrical spikes (3) 10–15 (25) mm long, 5–12 mm wide. Spikelets (30) 60–120, ellipsoid to oblong-ellipsoid, subterete, 2–4.5 mm long, (0.7) 0.8–1.2 mm wide; rachilla deciduous, with hyaline wings 0.3–0.4 mm wide. Scales 2 (–4), obovate,

Figure 4. *Cyperus svensonii*. **a**. plant; **b**. spikelet; **c**. achene.

mucronulate, 2.2–3.2 mm long, 1.2–2 mm wide, 3-nerved and greenish (rarely off-white) medially, 3–4 nerved and whitish (greenish-white when immature) laterally, persistent. Stamens 3; anthers oblong to oblong-ellipsoid, 0.4–0.5 (0.7) mm long, the connective apices at most 0.1 mm long. Styles (0.4) 0.6–0.8 (1.2) mm long; stigmas 3, 0.8–1.4 mm long. Achenes trigonous, oblong-ellipsoid to ellipsoid, 1.5–1.8 mm long, 0.6–0.7 mm wide, stipitate to substipitate, acuminate, apiculate, puncticulate, brown to reddish brown.

The known stations of *Cyperus svensonii* include the uplands of Chiapas, Guatemala, Honduras, and Nicaragua, in moist open situations in pine or oak forests, from (800) 1200–2300 m. The species is frequent throughout its range, especially in the montane valleys of Chiapas. Fruiting specimens have been collected from late June until November.

Cyperus svensonii is the only species of the genus in the New World that has densely cylindric *whitish* spikes. The densely cylindrical sessile spikes indicate a close relationship with *C. regiomontanus* Britt. In fact, several collections of this species were previously identified as "*C. regiomontanus.*" However, *C. svensonii* has ellipsoid to oblong-ellipsoid spikelets with obovate scales that are laterally whitish; *C. regiomontanus* has subulate-lanceolate spikelets and ovate scales that are laterally greenish to brownish. The two species are clearly allopatric: *C. svensonii* occurs in moist upland sites from (800) 1200–2300 m from Chiapas to Nicaragua; *C. regiomontanus* occurs in beach thickets and brushy pastures at or near sea level along the Pacific from Sinaloa, Mexico to Ecuador. The new species is named for Henry K. Svenson (1902–1986), lifelong student of the Cyperaceae and author of several works on the North American and neotropical genera of the family.

ADDITIONAL SPECIMENS: **Mexico.** CHIAPAS: Mpio. Tenejapa, paraje of Sibanil Ha', *Breedlove 6073D* (DS, NY); just W of San Cristobál, *King 3001* (MICH, TEX, UC); 20 km S of Tapilula, *Tucker 2630* (DUKE); near Huixtan, *Tucker 2209* (DUKE, ENCB); 20 km W of Comitán, *Tucker 2679* (DUKE, ENCB); San Benito, *Miranda 1889* (MEXU); 5 km N of Bochil, *Tucker 2635A* (DUKE). **Guatemala.** Depto. Huehuetenango, "Los Pinitos," *Steyermark 48192* (F, LL); Depto. Santa Rosa, Santa Rosa, *Heyde & Lux 3542* (M, MICH, US); Depto. Chimaltenango, near Chimaltenango, *Standley 59055* (F). **Honduras.** Depto. Morazán, Río Yeguare, *Glassman 1817* (F); Depto. Comayagua, vicinity of Siguatepeque, *Yuncker 5631* (F, GH, MICH); Depto. Morazán, Montaña Uyuca, *Molina R. 12789* (F). **Nicaragua.** Depto. Estelí, along road from Hwy. 1 to San Nicolás, *Kral 69478* (MO) and *Stevens 17860* (MO); Depto. Jinotega, Mesas Moropotente, *Henrich & Stevens 429* (DUKE, MO).

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BIOLOGICAL SURVEY
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THE TAXONOMIC POSITION OF *VACCINIUM SEMPERVIRENS* (ERICACEAE)

LEONARD J. UTTAL

ABSTRACT

Vaccinium sempervirens Rayner and Henderson is assigned to *Vaccinium* sect. Herpothamnus.

Key Words: *Vaccinium sempervirens*, sect. *Herpothamnus*, South Carolina

In the original description of *Vaccinium sempervirens* Rayner and Henderson (1980), a rare evergreen shrub of central South Carolina, the authors did not discuss the affinity of the species. They remarked on its resemblance to *Gaylussacia brachycera* (Michaux) Gray and *Vaccinium crassifolium* Andrews and that it had been misidentified as one or the other by different botanists. By assigning this species to section *Herpothamnus* (Small) Sleumer (Sleumer, 1941), confusion is eliminated.

Sect. *Herpothamnus,* as here circumscribed, consists of two low repent to repent-ascending shrubs (*Vaccinium crassifolium* and *V. sempervirens*) endemic to the coastal plain of the southeastern United States. The berry is shiny black to black-purple, round, sweet, 5-locular and 5-seeded, the seeds nutlike; the 5-lobed calyx is articulate with a very short pedicel, the corolla pink to white, urceolate with 5 short lobes, the flowers few in compact 1–4 flowered racemes usually borne in lower leaf axils, or sometimes terminal; leaf innovations are mostly from upper leaf axils. Both species have nodular lignous roots. *Vaccinium crassifolium* has strictly repent stems while in *V. sempervirens* the stems vary from repent to repent-ascending to strictly ascending. The two species may be separated by the following key:

1. Leaves 7–12 (20) mm long, 3–10 mm wide, about 20 per dm of branchlet; stem always repent, rooting at nodes .... *V. crassifolium*
2. Leaves 2.2–5.5 cm long, 1.3–3.0 cm wide, about 12 per dm of branchlet; stems repent and node-rooting to ascending, often tip-rooting .... *V. sempervirens*

Vaccinium crassifolium: sandy pinelands, barrens, or peaty pocosins, outer coastal plain from southeast Virginia to Georgia (the type species).

Vaccinium sempervirens: A proposed endangered species presently known only from Atlantic white-cedar communities on seepage slopes of Shealy's Pond, an impoundment in the sand hills of Lexington County, South Carolina, 4.5 miles southwest of Edmund, Congaree Girl Scout Camp and at Peach Tree Rock Preserve, a few miles to the east. The areas are under protective supervision of the Nature Conservancy. This site is isolated to the west of the range of *V. crassifolium.*

Conclusions are based upon (1) telephone consultation with Mr. D. A. Rayner, who knows the species well, (2) a tototype (VPI!), (3) the original description which includes excellent illustrations of the plant, and (4) personal observation in the field.

Vaccinium sempervirens is misidentified in Radford, Ahles, and Bell (1968) as *Gaylussacia brachycera* (Michaux) Gray, a species which does not naturally occur south of Virginia.

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I thank Mr. D. A. Rayner for freely sharing his store of information concerning this handsome new evergreen creeper of horticultural potential.

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DEPARTMENT OF BIOLOGY
VIRGINIA POLYTECHNIC INSTITUTE AND STATE UNIVERSITY
BLACKSBURG, VA 24061-0794

NEW ENGLAND NOTE

NOTES ON THE FLORA OF WINDHAM COUNTY, VERMONT

PETER F. ZIKA AND ELIZABETH H. THOMPSON

ABSTRACT

New stations or re-locations of historical stations for 15 species of rare plants have been found along the Connecticut and West Rivers in southeastern Vermont. *Platanthera flava* and *Rhexia virginica* are proposed as state threatened species.

Key Words: rare or threatened plants, Vermont flora

INTRODUCTION

"I have long felt sure that the extreme southeastern corner of Vermont, embracing the southern half of Windham County, would prove a rich field for botanical exploration. As it is not only next to Massachusetts but has a warm sandy soil, like that of eastern Massachusetts and southeastern New Hampshire, I expected to find a similar flora. Accordingly during my vacation this last summer I was located in Vernon, on the banks of the Connecticut [River], and was there about two months exploring the country around." Thus wrote A. J. Grout in an unpublished manuscript about his first extensive collecting trip to Windham Co. in 1895. Although John Carey and a few other botanists had collected in southeastern Vermont in the early 1800s (Oakes, 1842), Grout was the first to provide good specimens of the rarities of the area. (Of course, many of these are rare only in Vermont, and are abundant in southern and coastal New England.)

Grout discovered several important botanical areas in the 1890s, including South Pond and Sunset Lake in Marlboro, Kenny Pond in Newfane (now far less interesting due to a dam on the outlet), and Lily Pond in Vernon. The south-flowing Connecticut River divides Vermont from New Hampshire, on the eastern edge of Windham County, and in the broad valley of the Connecticut in Brattleboro and Vernon, Grout made many of his most interesting finds.

Around the turn of the century W. H. Blanchard and F. Blanchard made extensive collections in Windham Co., primarily in the floodplain of the Connecticut River. Their work and Grout's was incorporated in the Vermont floras of Brainerd et al. (1900) and Eggleston et al. (1915). Little has been published about the central Connecticut River flora since then, except in New Hampshire.

Neighboring Cheshire Co. in New Hampshire is floristically similar to Windham Co. (D. Boufford, unpublished manuscript). Crow and Storks (1980) pointed out that nearly 60 of New Hampshire's rare, threatened or endangered species are confined to the Connecticut River and its valley. Unfortunately for Vermont botanists, New Hampshire territory includes the width of the Connecticut River and its diverse aquatic flora.

The West River, a tributary of the Connecticut, drains most of the Green Mountain plateau and foothills in northern Windham Co. Below a massive flood control dam in Jamaica the West River is in a narrow valley with cobble- and boulder-lined grassy shores. The riverbanks have scattered thickets of *Alnus crispa* (Ait.) Pursh and *Salix sericea* Marsh., and an extensive population of *Sanguisorba canadensis* L. The last is wholly restricted to the shores of the West River in Vermont. Most of the rare plants in the West River drainage were first collected by L. A. Wheeler between 1911 and 1917 (e.g., Wheeler, 1912, 1913, 1914, 1919). The West is quite different from the Connecticut, and still provides excellent botanizing.

RECENT WORK

Contemporary collectors in Vermont have attempted to document extant populations for all the native plants reported in our flora. Using the Vermont checklist (Atwood et al., 1973) and label data on specimens at GH, HNH, MASS, MO, NEBC, SJFM, and VT, we attempted to re-locate all the rare native species recorded in Windham Co. (A rare plant is one known from ten or fewer contemporary sites statewide.) Rediscoveries and new stations through 1984 are reported below, as is the first Vermont record for the European adventive *Verbascum lychnitis* L.

Table 1 is a list of species known to occur in Vermont only in Windham Co. at the time of this writing. The majority of these are in the town of Vernon or along the banks of the West River.

Taxa we searched for unsuccessfully in Windham Co. (and elsewhere in Vermont) are given in Table 2. However, more field work is likely to show that many of these palnts are still extant in the county.

Table 1. Native Vermont species currently known to occur only in Windham Co.

Aster vimineus
Cassia nictitans
Crotalaria sagittalis
Hypericum gentianoides
Isoetes engelmannii
Juncus acuminatus
Juncus greenei
Lespedeza hirta
Panicum oligosanthes
Panicum rigidulum
Paspalum ciliatifolium
Platanthera flava
Polygala polygama
Polygala sanguinea
Quercus coccinea
Quercus ilicifolia
Rhexia virginica
Sanguisorba canadensis
Scirpus ancistrochaetus
Solidago odora
Tillaea aquatica
Triphora trianthophora
Viola lanceolata

Table 2. Native species documented at least once from Windham Co., with no known current stations in Vermont.

Arabis drummondii
Aristida longispica var. *geniculata*
Asclepias tuberosa
Astragalus alpinus
Baptisia tinctoria
Carex davisii
Cynoglossum boreale
Cyperus diandrus
Cyperus engelmannii
Cyperus ferruginescens
Desmodium rotundifolium
Eleocharis olivacea
Epilobium palustre
Eupatorium fistulosum
Fimbristylis autumnalis
Helianthus strumosus
Juncus militaris
Juncus secundus
Lechea minor
Lechea villosa
Lespedeza × *nuttallii*
Lespedeza steuvii
Myosotis laxa
Myriophyllum humile
Najas gracillima
Oenothera cruciata
Polygonum careyi
Pterospora andromedea
Rosa nitida
Rumex altissimus
Sagina decumbens
Sericocarpus asteroides
Sisyrinchium atlanticum
Subularia aquatica
Utricularia radiata
Xyris difformis

NOTEWORTHY FINDS

Chimaphila maculata (L.) Pursh In Vermont this species of dry woods has only been found near the Connecticut River. It is much more common to the south and west. The last Vermont collection was in 1903. In 1984 three stations were located: a small population at the base of Black Mountain, Dummerston (*Thompson & Rawinski 760* VT); about 50 plants in dry oak woods in South Vernon (*Zika 8406* VT); and a third site in Springfield, Windsor Co.

Cornus florida L. This attractive plant is at the northern limit of its range in the Connecticut River valley in southern Vermont and New Hampshire. A new station for the species was located on a rich wooded slope in Rockingham (*Thompson & Zika 8352* NEBC, VT). An estimated 20 mature fruiting trees were seen. About 200 young sprouts formed dense patches of ground cover in the area.

Corylus americana Walt. About 15 shrubs are in dry oak woods near the railroad right-of-way NE of Fox Hill, Vernon, Windham Co., Vt. (*Thompson & Zika 8383* VT). This is a new county record, and the only extant site east of the Green Mountains in Vermont.

Elymus villosus Muhl. ex Willd. A rare species in Vermont, last collected in 1922. An estimated 250 stems were found in a floodplain forest on the West River in Brattleboro (*Zika 7533* VT), growing with *E. wiegandii* Fern. and *Matteuccia struthiopteris* (L.) Todaro.

Elymus wiegandii Fern. Also a rare species in Vermont. About 50 stems were observed in a floodplain forest along the West River in Brattleboro (*Zika 7532* NEBC, VT), growing with the *E. villosus* and *Matteuccia struthiopteris.*

Juncus marginatus Rostk. A small population is on the sandy shore of a small unnamed pond in Rockingham, Windham Co., Vt (*Zika 7797* VT). A larger colony is present on the banks of the West River, on ledges and in peaty wet soil (*Thompson & Zika 8360* VT). Only one other station in Vermont is known to be extant, a small colony on the banks of the Huntington River in the Champlain Valley.

Muhlenbergia sobolifera (Muhl.) Trin. About 100 stems are on a dry rocky forested slope in Rockingham (*Thompson & Zika 8353* VT). This is the first record east of the Green Mountains in Vermont.

Muhlenbergia tenuiflora (Willd.) BSP. About 500 plants are on a dry rocky wooded slope in Westminster (*Thompson & Zika 8348* VT). This is the only extant population in eastern Vermont.

Platanthera flava (L.) Lindl. A total of 100 plants was found in the towns of Newfane and Brookline on a short stretch of the West River (*Zika 7553, 7554* VT). Sterile as well as flowering individuals were inconspicuous, mixed in with the dense low herbs on the cobble shore.

Podostemum ceratophyllum Michx. The status of this submerged aquatic in Windham Co. has long been unclear. It was first reported by C. C. Frost from Brattleboro, presumably in the West River (Eggleston et al., 1915), but no vouchers were located and recent searches failed to find the species in the city limits. *Podostemum* was collected in the West River in 1907 in the town of Jamaica by F. Dobbin (Dobbin, 1907), and was visited there by botanists through the 1920s. In recent decades Dobbin's station was not relocated. The extreme flow fluctuations caused by the installation of two flood-control dams upriver of the Jamaica site were believed to have destroyed the population (Countryman, 1978; Philbrick & Crow, 1983). A new station was discovered on one of the numerous short rapids on the West River, downriver of Jamaica in Newfane. Between 30 and 60 cobblestones in the deepest part of the riverbed were covered with *Podostemum* (*Zika 7562* VT).

Quercus ilicifolia Wang. Scrub oak is restricted to Windham Co. in Vermont. A colony of about 50 vigorous shrubs was located under a powerline clearing on the west side of Black Mountain, near the West River (*Zika 7544* VT). Subsequent field work showed the species was scattered on the southern and western slopes of Black Mountain, above the powerline, to an elevation of 1100 feet (*Thompson & Rawinski 758* NEBC). This is the only known extant population in Vermont.

Rhexia virginica L. Vermont's only extant station is at Lily Pond in Vernon, where about 200 plants are concentrated on a short, grazed stretch of the northern shoreline (*Zika 6534* VT).

Stellaria alsine Grimm Three colonies of 100 to 300 stems were found in springs along a small unnamed creek between Vt. Route 142 and the Connecticut River in Vernon (*Thompson & Zika 8373* VT). The only other extant colony in Vermont is in Ludlow, Windsor Co.

Verbascum lychnitis L. A weed introduced from Europe and known mostly to the south and west of Vermont. A small colony was found in 1982 on the west side of U.S. Route 5 in Dummerston, just south of the Putney town line (*Zika 6266* VT). This is the first Vermont record of this species.

Viola lanceolata L. Although a common and somewhat weedy species in southern New England, lance-leaved violet is currently quite rare in Vermont. The only extant population is about 20 plants on barren ground at the rim of a borrow pit on Lily Pond Road in Vernon (*Zika 7080* VT). A few more clumps can be found nearby on the shore of Lily Pond. The entire population may be threatened by grazing cows.

THREATENED STATUS OF *PLATANTHERA FLAVA* AND *RHEXIA VIRGINICA*

Platanthera flava was formerly a widespread species in Vermont, with 25 historical stations represented in herbaria. Eggleston et al. (1915) considered *P. flava* locally common in Vermont; Dole (1937) listed it as occasional. Only two historical stations along the West River in Windham Co. have been seen in recent years. Many historical stations in the Lake Champlain valley have disappeared. The cause of the apparently drastic decline of the species in Vermont is unknown.

One of the two historical stations for *Rhexia* was discovered by L. Henry Potter in Wallingford, where a housing development has since destroyed the colony (Potter, pers. comm.). The second station, in Vernon, is extant but is threatened by grazing cows.

Due to declining populations, *Platanthera flava* and *Rhexia virginica* are recommended for threatened species status in Vermont (10 V.S.A., Chapter 123).

ACKNOWLEDGMENTS

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P. F. Z.
PRINGLE HERBARIUM
BOTANY DEPARTMENT
UNIVERSITY OF VERMONT
BURLINGTON, VT 05405

E. H. T.
VERMONT NATURAL HERITAGE PROGRAM
THE NATURE CONSERVANCY
138 MAIN ST.
MONTPELIER, VT 05602

BOOK REVIEW

Proctor, G. R. 1985. *Ferns of Jamaica.* vi + 631 pp. British Museum (Natural History), London (£50.00).

The *Ferns of Jamaica* is the culmination of over thirty years of study by the author of the native and naturalized pteridophytes of the island. The concise descriptions of 609 species, varieties and hybrids along with notes on their distributions and habitats will serve as an invaluable reference for those wishing to identify Jamaican pteridophytes for a long time to come.

Seventy-five of the eighty-three genera recognized are illustrated. Especially noteworthy are the fine line drawings of twenty of the twenty-eight species of *Elaphoglossum* by Charles D. Clare. Other large and difficult genera such as *Adiantum, Thelypteris, Asplenium, Diplazium, Polypodium* and *Grammitis* received considerably fewer illustrations by comparison.

Twenty maps plotting the distributions of thirty-five species are interspersed throughout the text. The author does not indicate why these species are mapped whereas the other 544 are not.

A conspectus of the major taxa is included rather than a key to families. Once a plant has been identified to family, there are keys to subfamily, genus and species. The key to the subfamilies of Polypodiaceae *sens. lat.* appears to be workable for the most part; however, it is not possible to arrive at the Athyrioideae when keying out *Diplazium plantaginifolium.*

The systematic treatment is an interesting blend of a rather liberal philosophy in recognizing pteridophyte entities with a conservative approach to recognizing genera and families. All ferns with slender-pedicellate sporangia which have a vertical annulus are placed in the Polypodiaceae *sens. lat.* While some might argue that the subfamilies should be raised to families, the question of rank seems less important than the composition of the groups. In most cases Proctor's placement of genera into higher taxa agrees with that of other authors (e.g. Christensen, 1938; Holttum, 1949; Crabbe et al., 1975; and Tryon and Tryon, 1982), however, a few assignments are worthy of mention. All of the above authors place *Saccoloma* in the dennstaedtioid ferns. Proctor places it in the *Lindsayoideae.* Similarly, all align the genus *Hemidictyum* with the athyrioid ferns.

Proctor places it with the asplenioid ferns. Since descriptions of the subfamilies are omitted and since it is difficult to determine the characters of the subfamilies from the key (one subfamily is keyed out in nine different places), one cannot determine what evidence the author considered in reaching these systematic conclusions.

Despite these criticisms, the book stands as a major contribution to tropical American Pteridology. Anyone interested in New World ferns or in the flora or phytogeography of the Caribbean would find this book worth the investment.

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DAVID S. CONANT
DEPARTMENT OF NATURAL SCIENCE
LYNDON STATE COLLEGE
LYNDONVILLE, VERMONT 05851

NEBC AWARD FOR THE SUPPORT OF BOTANICAL RESEARCH IN NEW ENGLAND, U.S.A.

Debra A. Dunlop was selected to receive the 1986 New England Botanical Club award in support of botanical research in New England for her proposal "Biosystematics of *Carex* section *Scirpinae* (Cyperaceae)." Ms. Dunlop, a Ph.D. candidate working with Dr. Garrett E. Crow at the University of New Hampshire, will use the award to travel to alpine areas of New York, Vermont, New Hampshire and Maine and to limestone and serpentine sites in southeastern Canada to collect material for anatomical, cytological and micromorphological studies and for crossing experiments.

The New England Botanical Club will again offer an award of $1000 in support of botanical research to be conducted in the New England region during 1987. This award is made to stimulate and encourage botanical research on the New England flora and to make possible visits to the New England region by those who would not otherwise be able to do so. The award will be given to the graduate student submitting the best research proposal dealing with field studies in systematic botany and plant ecology, but proposals for research in other areas of botany will also be considered. This award is not limited to graduate students at New England institutions, nor to members of the New England Botanical Club. Papers based on this research must acknowledge the NEBC's support, and it is encouraged that they be submitted to *Rhodora,* the Club's journal, for possible publication—subject to standard review processes.

Applicants should submit a proposal of no more than three double spaced pages, a budget (the budget will not affect the amount of the award), and a curriculum vitae. Two letters, one from the student's major professor, in support of the proposed research are also required. Proposals and supporting letters should be sent before 28 February 1987 to:

Awards Committee
The New England Botanical Club
22 Divinity Avenue
Cambridge, MA 02138

The recipient of the award will be notified by 30 April 1987.

THE 1986 JESSE M. GREENMAN AWARD

The 1986 Jesse M. Greenman Award has been won by David H. Lorence for his publication "A Monograph of the Monimiaceae (Laurales) in the Malagasy Region (Southwest Indian Ocean)," which appeared in the *Annals of the Missouri Botanical Garden,* volume 72, number 1. The publication is derived from a Ph.D. dissertation from Washington University under the direction of Alwyn H. Gentry. This comprehensive account of fifty-five species, all endemic to the region, is based on herbarium records and extensive fieldwork. It includes information on pollination syndromes in relation to floral morphology, cytological investigations, population biology, vernacular names, and economic uses.

The Award is named for Jesse More Greenman (1867–1951), who was Curator of the Missouri Botanical Garden Herbarium from 1919 until 1943. A cash prize of $250 is presented each year by the Garden, recognizing the paper judged best in vascular plant or bryophyte systematics based on a doctoral dissertation that was published during the *previous* year. Papers published during *1986* are now being considered for the 19th annual award, which will be presented in the summer of 1987. Reprints of such papers should be sent to:

Greenman Award Committee
Department of Botany
Missouri Botanical Garden
P.O. Box 299
St. Louis, MO 63166-0299, U.S.A.

In order to be considered for the 1987 award, reprints must be received by 1 July, 1987.

MEETING ANNOUNCEMENT
NEW ENGLAND BOTANY GRADUATE STUDENTS

The second New England Botany Graduate Student Meeting will be hosted by the Department of Botany and Plant Pathology at the University of New Hampshire, Durham, NH on Saturday 14 March 1987. Attendance is open to all. Paper presentations will be largely restricted to graduate student research (completed or in progress) representing all areas of botany (systematics, ecology, reproductive biology, anatomy, physiology, etc.). Time slots for paper presentations are limited and prior registration is required. Abstracts are due by 15 February 1987. For additional information and abstract forms, contact:

Debra Ann Dunlop
Department of Botany and Plant Pathology
Nesmith Hall
University of New Hampshire
Durham, NH 03824
(603) 862-3531

WILLIAM WIRT CALKINS
MOSS AND LICHEN COLLECTIONS

The Chicago Academy of Sciences houses the moss and lichen collections of William Wirt Calkins. There are several thousand specimens, including 12 exsicatti volumes. The locales represented include Florida, Illinois, Virginia, Ohio and others. The collections were made between 1870 and 1910. This collection has not appeared in scientific literature and is available for study. Inquiries should be sent to:

Ron Vasile
c/o Chicago Academy of Sciences
2001 North Clark Street
Chicago, IL 60614

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The editors of RHODORA are grateful to each of the following specialists for their participation in the review process.

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