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Review Article

Dengue outbreaks and the geographic distribution of dengue vectors in Taiwan: A 20-year epidemiological analysis

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ARTICLE INFO

Article history:
Received 10 May 2018
Accepted 14 June 2018
Available online 9 November 2018

Keywords:
Dengue outbreaks
Dengue vectors
Diapause
Geographical distribution
Overwintering
Taiwan

ABSTRACT

Dengue fever is an important mosquito-borne viral infectious disease that mostly occurs in tropical and subtropical areas of the world. According to epidemiological data from the Center for Disease Control of Taiwan, more than 98.62% of outbreaks of indigenous total dengue cases were reported in the southern part of Taiwan. Southern Taiwan is an aggregate area encompassing Tainan, Kaohsiung, and Pingtung, all of which are located below the Tropic of Cancer (23°35′N). With a few exceptions, dengue outbreaks mainly occur in southern Taiwan which is highly associated or overlaps with the prevalence of *Aedes aegypti*. *A. aegypti* is presumed to be absent from the northern part of Taiwan, while *Aedes albopictus* breeds in areas throughout the island. According a collection of 20 years of epidemiological data from Taiwan, the inability of *A. aegypti* to survive the winter weather in northern Taiwan may account for its restricted geographical distribution and that of dengue outbreaks it transmits. *A. aegypti*, unlike temperate strains of *A. albopictus*, lacks embryonic diapause signaled by a short photoperiod which thus reduces its cold-hardiness. Therefore it is intolerant of low temperatures that frequently accompany rains and unable to survive during winter in the northern part of Taiwan.

Dengue fever is a mosquito-borne viral disease with increasing global importance because of the rapidly spreading expansion of the infection, inefficient control of mosquito vectors, and the heavy disease burden [1]. It is caused by the dengue virus, a member of flaviviruses belonging to the family Flaviviridae [2]. The virus can be divided into four antigenically related serotypes (D1–D4) of its etiological agent. The dengue virus generally causes clinical symptoms indistinguishable among serotypes [3]. Illness including dengue fever and occasionally severe forms of the disease, such as dengue hemorrhagic fever and dengue shock syndrome, are reported in most patients [4]. In addition, encephalitic

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Peer review under responsibility of Chang Gung University.
https://doi.org/10.1016/j.bj.2018.06.002

symptoms may be seen in some cases [5,6]. Currently, dengue fever is endemic to more than 125 countries [7], especially tropical and subtropical regions, such as Southeast Asia and Latin Americas [8,9].

The dengue virus is maintained in nature via a cycle transmitted by *Aedes* mosquitoes between humans or monkeys for the jungle cycle [10] [Fig. 1]. Transovarial or vertical transmission in mosquitoes themselves has also occasionally been observed [11,12]. This reflects that the dengue virus is sustained by alternate replication in mosquitoes and humans [13]. Most important vectors involved in the transmission of the dengue virus include *A. aegypti* and *A. albopictus*, both of which are members of the subgenera *Stegomyia* [14], because of susceptibility to the virus and a high efficiency of transmission to humans [4,15,16]. Of these, *A. aegypti* originated from Africa, but is now prevalent in most tropical and subtropical regions of the world [17]. *A. albopictus* is a species endemic to Southeast Asia [14]; nowadays, it has expanded to a broad range of the world including Europe and Africa since it was first introduced into North America via the trade in used tires [18–22].

Dengue fever has become endemic in Taiwan; however, most outbreaks were reported from the southern part of the island, in particular, Tainan City, Kaohsiung City, and Pingtung County. This review provides information elucidating this fascinating feature. In addition to describing a brief history of dengue outbreaks in Taiwan, evidence of a skewed prevalence of dengue cases and a compatible distribution of *A. aegypti* with dengue outbreaks in Taiwan are also addressed. Features including overwintering of *A. albopictus* and a lack of embryonic diapause which may determine the overwintering ability of *A. aegypti* are also discussed; these thus contribute to the distribution of dengue vectors and the outbreaks they transmit in Taiwan.

A brief history of dengue outbreaks in Taiwan

Dengue fever has been recognized in the world for perhaps hundreds of years [23]. During the first half of the 20th century, most outbreaks in the world were reported from East Asia and Western Pacific countries [24]. Meanwhile, two large-scale dengue outbreaks, recorded in 1915 and 1942, spread throughout the island of Taiwan [25,26]. It is estimated that the former caused 1.7 million infections out of a total population of 3.5 million (approximately 50%), while the latter resulted in 5 million infections among 6 million residents (>80%). However, severe dengue epidemics were absent from Taiwan after World War II (WWII), as seen in many other countries of the world. This is also believed to have been the result of worldwide programs for malaria control in areas in which both malaria and dengue were simultaneously endemic [27,28].

The reemergence of dengue fever after WWII in Taiwan first occurred in 1981, as an outbreak mainly caused by the dengue 2 virus, and which resulted in an infection rate of >80% (13,000 reported cases/15,000 residents) on Liu-Chiu Islet, Pingtung [29,30]. Following this outbreak, a larger outbreak (mainly caused by the dengue 1 virus) appeared in 1987 through 1988 [31], causing approximate 5000 indigenous cases in Kaohsiung which is a city neighboring Pingtung [32]. Thereafter, dengue outbreaks accompanied by occasional severe forms of the disease appeared more frequently and

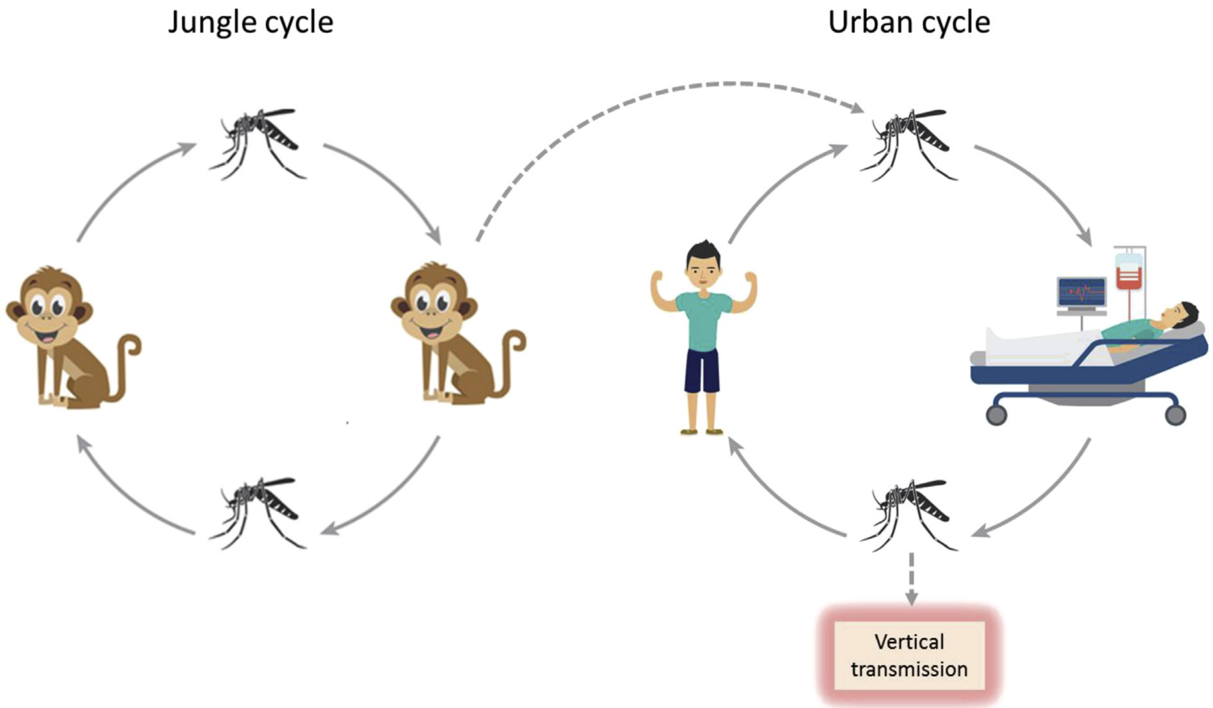

Fig. 1 The dengue virus is naturally transmitted by *Aedes* mosquitoes between humans or monkeys in the jungle cycle. Transovarial or vertical transmission in mosquitoes themselves may also occasionally occur.

actually became one of the endemic infectious diseases in Taiwan [33].

The time gap of the reemergence of dengue outbreaks for almost four decades in Taiwan is attributed to: (1) a fading of herd immunity created by previous outbreaks before 1946; (2) termination of residual spraying programs with dichlorodiphenyltrichloroethane (DDT) for malaria control in early 1973 [34]; (3) the rapid increase in international traffic by jet airplanes [35]; (4) canceling of a ban on traveling abroad in 1987; and (5) initiation of recruitment of allied laborers mainly from Southeast Asian countries in 1989 [36].

Skewed prevalence of dengue cases in Taiwan

According to a database covering the period from 1998 to 2017 based on information from the Taiwanese Center for Disease Control (CDC) (website: https://nidss.cdc.gov.tw/ch/NIDSS_DiseaseMap.aspx?dc=1&dt=2&disease=061), a relatively few indigenous dengue cases were found in northern and central parts of the island despite annual imported cases in the same regions being obviously greater than those recorded in the southern part including Tainan, Kaohsiung, and Pingtung [Fig. 2]. Statistically, 73,896 of 74,959 (98.62%) confirmed indigenous cases were reported from the southern part of Taiwan, while only 622 of 2703 nationally imported cases (23.01%) were reported for the same region [Table 1]. Major dengue outbreaks reported in the past three decades mostly appeared in locations south of the Tropic of Cancer (23°35′N) which geographically divides the island into two climatic regions, *i.e.*, tropical and subtropical. Apparently, only the environment with a tropical climate is suitable for dengue virus transmission by the mosquito vector and establishment of dengue outbreaks [37].

Compatible distribution of *A. aegypti* and dengue outbreaks

In many part of the world, dengue outbreaks mostly occur in places with an abundance of *A. aegypti*, while they are also only occasionally reported from places where *A. albopictus* is distributed [38,39]. In surveillance conducted for the 1987–1988 dengue outbreak in Kaohsiung and Pingtung, the

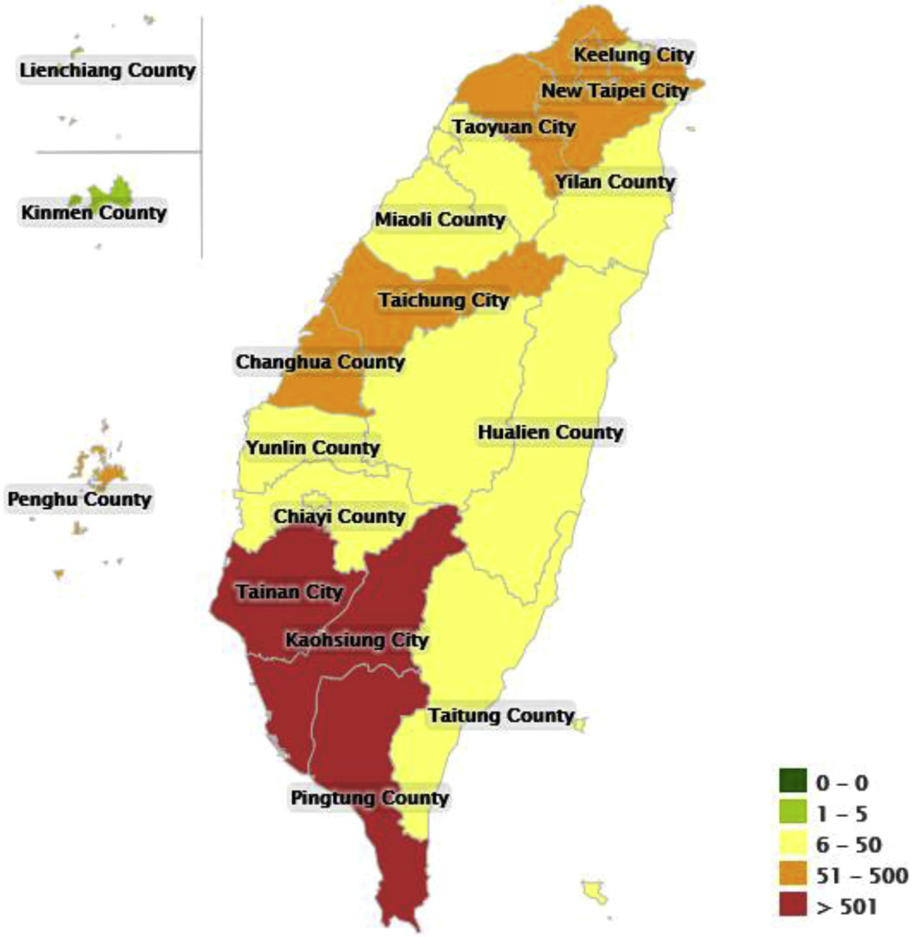

Fig. 2 By focusing on statistics of dengue cases accumulated from 1998 to 2017 in Taiwan, it was determined that most (98.62%) confirmed indigenous cases were reported from southern Taiwan, especially Tainan, Kaohsiung, and Pingtung. All of these areas are located south of the Tropic of Cancer (23°35′N), *i.e.*, a region with a tropical climate (Data from the Center for Disease Control, Taiwan).

Table 1 According to a database of dengue cases covering the period 1998–2017, 73,896 of 74,959 (98.62%) confirmed indigenous cases (in blue) were reported from south of the Tropic of Cancer (23°35′N) in Taiwan including Tainan, Kaohsiung, and Pingtung (in red), while only 622 of 2703 imported cases nationwide (23.01%) were reported from the same area.

Region	**Imported Cases**	**Indigenous Cases**
Taipei City	500	182
Taichung City	303	115
Tainan City	**184**	**26,539**
Kaohsiung City	**343**	**45,319**
Keelung City	27	9
Hsinchu City	29	25
Chiayi City	16	31
New Taipei City	443	170
Taoyuan City	330	83
Hsinchu County	73	29
Yilan County	31	11
Miaoli County	51	12
Changhua County	102	65
Nantou County	46	17
Yunlin County	49	36
Chiayi County	34	50
Pingtung County	**95**	**2,038**
Penghu County	3	144
Hualien County	25	14
Taitung County	13	38
Kinmen County	6	3
Lienchiang County	0	2
Nation-wide	**2,073 (23.01%)**	**74,932 (98.62%)**

Based on information from the Center for Disease Control (CDC), Taiwan.

virus was isolated from nine pools of *A. aegypti* females, but none from eight other species of mosquitoes collected from houses located in epidemic regions [40]. Moreover, mosquito sampling performed in and around households of patients was shown to have a predominance of *A. aegypti* (95.15%) vs. *A. albopictus* (4.85%) even in places where both species of mosquito were distributed [41]. In a test using an intrathoracic microinjection or oral-feeding approach, *A. albopictus* was less susceptible to the dengue virus [5,42]. This further indicates that *A. aegypti* is a more-efficient dengue vector, especially because it is the species that possesses an anthropophilic biting preference. Rather importantly, the confirmed case number was shown to have a positive relationship with the Breteau index of *A. aegypti* in areas with aggregated cases [43]. This, in turn, reveals that the roles of the two dengue vectors in dengue transmission in Taiwan were eventually able to be discriminated [37].

A study carried out in Singapore further showed that infected *A. aegypti* appeared much earlier, compared to *A. albopictus*, approximately as early as 6 weeks before the occurrence of an outbreak [44]. We assume that *A. aegypti* may initiate an early outbreak, while *A. albopictus* participates in the latter phase of the outbreak, resulting in establishment and subsequent expansion of the outbreak [37]. Looking back at all outbreaks reported from Taiwan in the past two decades, according to a dataset of the Taiwanese CDC, *A. aegypti* was undoubtedly more critical to the transmission of dengue viruses than was *A. albopictus*. Perhaps dengue outbreaks can only occur when *A. aegypti* exists or it is the predominant species [45].

In Taiwan, *A. albopictus* breeds throughout the island in areas below 1,000 (occasionally 1,500) m in elevation [46]. In contrast, the distribution of *A. aegypti* is limited to south of the Tropic of Cancer, generally along the southwestern coastal belt [43] [Fig. 3]. Looking at the geographical distribution of *A. aegypti*, it is fully compatible with the occurrence of dengue cases, mostly around the southern part of the island [47–49].

Overwintering of *A. albopictus*

A. albopictus is an endemic species of mosquito in Southeast Asia; however, it also breeds in various parts of temperate areas of Asia, including China, Japan, and South Korea [50]. This reveals that *A. albopictus*, at least some strains, is more cold-hardy, leading to its ability to preserve and thus maintain a sustainable population in the field [51]. Diapause (a state of developmental arrest), an important character seen in many other insects, helps organisms pass a harsh weather [52,53]. The mosquito *A. atropalpus* was demonstrated to survive the cold weather by means of diapause-enhanced cold-hardiness [54]. In fact, diapause was also shown to exist in certain strains of *A. albopictus*, serving as one factor favoring its overwintering, particularly in temperate areas [55].

Diapause in mosquito overwintering was observed to occur in different developmental stages, *i.e.*, adults, larvae, eggs, or a combination, depending on the species of mosquito [56]. Of these, egg or embryonic diapause seems to be more common as shown in temperate strains of *A. albopictus* [57]. The embryo during diapause is confined inside the chorion of the egg, resulting in insensitivity of a response to any climatic stimuli for hatching [52]. Nearly 50% of diapausing eggs deposited by engorged females are able to survive the winter in temperate China, and its population density declines during the winter [58]. Apparently, fluctuations of *A. albopictus* populations are highly associated with seasonal embryonic diapause of strains in temperate regions and possibly also in subtropical regions [59].

In addition to temperature, photoperiod is also a critical climatic factor involved in diapause induction [60]. It was noted that most diapausing eggs of *A. atropalpus* are deposited in fall [54], suggesting that shorter daylight serves as a signal of seasonal change and subsequently drives induction of mosquito diapause. In the mosquito *Aedes triseriatus*, there was a significant interaction between temperature and photoperiod on induction of egg diapause [60]. It is presumed to work by influencing the prediapause stage of developing mosquitoes [61]. A study of *A. albopictus* in Japan also showed that egg diapause begins in late fall, which is the transition period between favorable and unfavorable seasons for

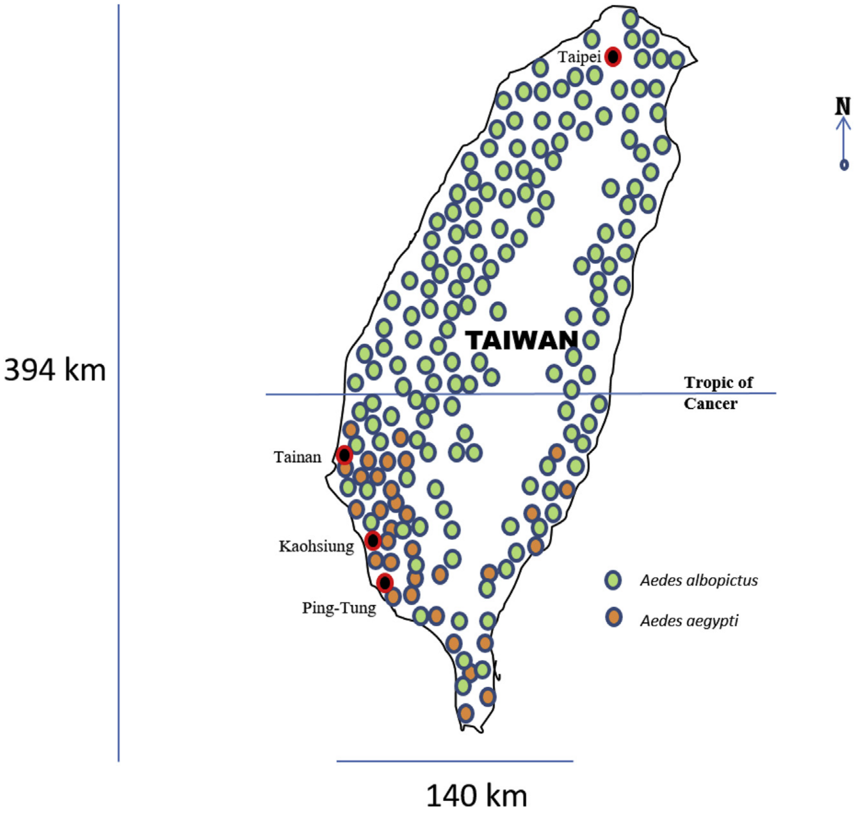

Fig. 3 Estimated distributions of dengue vectors, *i.e.*, *Aedes aegypti* and *A. albopictus* in Taiwan. The former species breeds in abundance south of the Tropic of Cancer (23º35′N), while the latter is extensively distributed in areas of less than 1,000 m (occasionally 1,500 m) in elevation throughout the island (Data from the Center for Disease Control, Taiwan).

mosquito survival [62]. Physiologically, the short photoperiod beginning in fall seems to be an essential signal required for induction of egg diapause, which enhances the mosquito's ability to survive lower temperatures in winter. Taken together, effective induction of diapause in eggs laid by *A. albopictus* provides a sufficient period of time to complete development of one mosquito generation, leading to seasonal synchronization of eggs hatching the following year [63].

Laboratory observations revealed that *A. albopictus* in Taiwan is unable to develop at a temperature below 15 °C [64]. However, *A. albopictus* can maintain population breeding in the north, at which time temperatures lower than 10 °C occur much longer than in the south (website: https://www.cwb.gov.tw/V7/climate/monthlyMean/Taiwan_txminle10day.htm). It seems that *A. albopictus* in Taiwan may be more similar to strains breeding in temperate regions, *e.g.*, Japan, that present cold hardiness via egg diapause. Diapause may be induced by the signal of a shorter photoperiod in fall, which occurs in October each year (https://www.cwb.gov.tw/V7/climate/monthlyMean/Taiwan_sunshine.htm). Moreover, mosquitoes such as *A. albopictus* in tropical regions may have a character of quiescence which is non-seasonal dormancy, helping them survive high temperatures [65]. It seems that *A. albopictus* is evolutionarily successful, as it can sustainably distribute throughout the island of Taiwan in both summer and winter [66,67].

Lack of embryonic diapause in *A. aegypti*

According to a recent study in Taiwan, a land surface temperature of 13.8 °C is the critical limit for breeding of *A. aegypti* larvae in the field [68]. Although the annual average temperature in Taiwan is 22 °C with a range of 12–30 °C (website: https://www.chinahighlights.com/taiwan/weather.htm), it can approach 8 °C or lower in winter in northern Taiwan. Obviously, this weather is unsuitable for the sustained development of mosquitoes. Although *A. albopictus* may have strains that possess egg diapause to enhance their cold hardiness, a lack of this character in *A. aegypti* eggs may cause an intolerance for low temperatures in winter. Although quiescence characterized by slowed metabolism was also addressed in *A. aegypti* in unfavorable environments, it seems to work specifically in conditions of low humidity and high temperature in summertime [69].

More significantly, mosquito larvae that emerge following a rainfall are much less tolerant of temperatures below 10 °C [70]. *A. albopictus* in the French Riviera is highly dependent on egg diapause driven by temperature and rainfall to maintain its population dynamics [71]. This implies that mosquito overwintering could succeed depending on the combined effects of multiple climatic factors. A temperature of <13 °C is frequently accompanied by a consecutive rainy period in winter in northern Taiwan (website: www.timeanddate.com/

weather/taiwan/kaohsiung/climate). It is obvious that the weather in northern Taiwan is unfavorable for *A. aegypti* larvae to develop sustainably. Warm and dry climates eventually favor *A. aegypti* maintaining higher survival rates [69]. Undoubtedly, development-regulating dormancy, such as egg diapause, determines the status of *A. aegypti* being abundant only in southern, not in northern, Taiwan.

Conclusions

During the past three decades in Taiwan, most dengue outbreaks were reported from the south, *i.e.*, Tainan, Kaohsiung, and Pingtung, regions with a tropical climate on the island. The distribution of dengue cases is extremely compatible with breeding areas of *A. aegypti*, rather than those of *A. albopictus*. This suggests that *A. aegypti* is critically important as a vector that contributes to most outbreaks in Taiwan. The absence of *A. aegypti* from northern Taiwan is suggested to result from an intolerance of cold and rainy conditions during the winter. Unlike temperate strains of *A. albopictus*, *A. aegypti* lacks photoperiod-triggered embryonic diapause, resulting in reduced cold-hardiness and a consequent failure to survive the winter in northern Taiwan.

Conflicts of interest

The author declares no conflicts of interest.

Acknowledgments

The author would like to thank Mrs. I-Chuan Chen for assistance with figure-sketching. This work was supported by grants from the Ministry of Science and Technology, Taiwan (MOST103-2320-B-182-029-MY3) and Chang Gung Memorial Hospital (CMRPD1F0321~3).

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