Morphometric and taphonomic study of a ray-finned fish assemblage (*Lepidotes buddhabutrensis*, Semionotidae) from the Late Jurassic–earliest Cretaceous of NE Thailand

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Abstract: Most Mesozoic vertebrate species are represented by scarce and incomplete specimens, preventing statistical studies of morphometric features. Moreover, rich vertebrate assemblages are rarely excavated in conditions that allow taphonomical studies. *Lepidotes buddhabutrensis* is a common species found in the Late Jurassic–Early Cretaceous locality of Phu Nam Jun, Phu Kradung Formation, in NE Thailand. Individuals, collected during systematic excavation since 2002, show great variations in preservation states and body postures. In this paper we study the mode of variation of morphometric features of the fish population, the growth mode, and the relationship between morphology and size. We assess the range of variation in preservation and taphonomy, based on arbitrarily defined scales, to test if vertical variations occur in the sample of individuals within the site. We test possible favoured orientation of specimens within the assemblage. In contrast to preliminary field observations, statistical analyses show that all individuals belong to a single Gaussian population and that gross morphological shape variations are related only to size during fish growth. *L. buddhabutrensis* shows a positive allometric growth for the pectoral to dorsal, and pectoral to anal fin distances, and a negative allometric growth for the unpaired fins (dorsal and anal fins lengths). We detected no relationships between the vertical location of the fishes within the fossiliferous deposit and the body shape of the specimens, nor between the state of preservation and the taphonomy, but there are significant differences in the state of preservation according to the position of the fishes in the fossiliferous deposit. The occurrence of a single Gaussian population and the absence of morphological and preservational variations through the depositional column are evidence that the fish assemblage is probably the result of a single mass mortality event. The apparent diversity in morphology is probably due to variations in the mode of preservation. The fish appear to have been oriented by a current at the time of deposition at the top of the fossiliferous deposit only.

Supplementary material: Primary measurements are available at http://www.geolsoc.org.uk/SUP18347.

The Mesozoic sediments from the Khorat Plateau, NE Thailand, have yielded an abundant vertebrate assemblage ranging in age from the Late Triassic to the Early Cretaceous (Buffetaut & Suteethorn 1998). The bony fish record is rather rich, but mainly represented by isolated teeth, scales and tooth plates (Martin & Ingavat 1982; Martin et al. 1984; Cavin et al. 2009). Numerous isolated

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scales and some teeth have been referred to semionotid fish. In 1998, fragments of articulated and well preserved ganoid fish were discovered at a locality named Phu Nam Jun in Tambon Lao Yai, Amphoe Kuchinarai, Kalasin Province (Fig. 1). Between 2002 and 2008, systematic excavations at this site produced more than 200 fish specimens, most referable to *Lepidotes buddhabutrensis* Cavin *et al.* 2003. This freshwater semionotiform fish, with no crushing dentition, shows derived characters in its buccal apparatus, very distinct from the type species, *L. elvensis* (de Blainville 1818), indicating that the Thai species may belong to a different genus. Its gross morphology, reminiscent of a cyprinid fish, and its lower jaw dentition with small horizontally oriented teeth suggest a vegetarian diet, possibly by scratching food on the substrate. So far no study has investigated whether the fish assemblage represents one or several populations, although field observations led Cavin *et al.* (2004) to suggest that two morphotypes, a deep one and a shallow one, possibly occur together. The aim of this paper is to test the intraspecific variation of the fossil fish assemblage of *L. buddhabutrensis* in the locality of Phu Nam Jun, and to examine some of the taphonomical processes involved in the formation of the fossiliferous deposit.

Although not all specimens have yet been prepared and although many more specimens probably remain to be uncovered at the site, we have performed this preliminary study to test field observations and to assess the scientific potential for future studies.

**Geological setting**

The Phu Nam Jun locality is situated in the upper part of the fluvial and lacustrine Phu Kradung Formation (Buffetaut *et al.* 1994), which is the lowest formation of the Khorat Group as currently defined. Post-Triassic Mesozoic deposits of the Khorat Group have long been regarded as Jurassic in age. However, palynological studies (Racey *et al.* 1994, 1996; Carter & Bristow 2003) suggest younger ages for most of the formations included in that group, although the Phu Kradung Formation has yielded inconclusive palynological evidence so far. According to age constraints provided by the overlying formations, the Phu Kradung Formation may be either Late Jurassic or earliest Cretaceous in age.

Changes in lithology occur in the fossiliferous deposit of the Phu Nam Jun site, but we cannot follow them laterally. They may represent lateral variations within a single large depositional event or discrete depositional episodes. So far, sedimentological field observations do not allow us to make a decision on that issue. The single visible clear lithological change is a greenish sandy deposit at the bottom of the excavated area but its lateral extension and 3D structure are unknown. The upper part of the fossiliferous deposit consists of a maroon mudstone with sandstones lens, mica and concretions.

**Materials and methods**

All specimens are housed in the Sirindhorn Museum, Sahat Sakhan District, Kalasin Province, Thailand. The specimens were prepared from their upper side with air-pens and scalpels in the Sahat Sakhan Dinosaur Research Centre. Sixty-one individuals were used in morphometric and meristic analyses and 92 individuals in studies dealing with preservation modes and body postures. The remaining specimens are yet to be prepared.

**Measurements**

The position and orientation of each individual *L. buddhabutrensis* were recorded on a map prior to being removed in plaster jackets. Measurements and meristic features of the body were recorded following McCune’s method (McCune 1987; Fig. 2). The term ‘preservation mode’ corresponds here to the state of decay before fossilization while ‘taphonomic state’ corresponds here to the body posture and not the state of decay. These two parameters have been divided into arbitrarily defined qualitative scales, comprising four classes of preservation and four classes of taphonomic.

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**Fig. 1.** Map of NE Thailand showing the Phu Kradung outcrops in black and the Phu Nam Jun locality (open circle).
states, defined as follow:

**Preservation (Fig. 3)**

State 1: very well preserved: the body of the fish is complete and articulated; the fins are preserved (although rarely completely).

State 2: well preserved: the body of the fish is articulated and almost complete, sometimes a few scales are missing; the fins are incompletely preserved but their position on the body can be accurately identified.

State 3: not well preserved: the fish is partly articulated but incomplete; fragments of fins may be preserved but their position on the body cannot be identified with certainty.

State 4: badly preserved: only fragments of the body are preserved; the outline of the fish is not always recognizable.

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**Fig. 2.** Morphometric methods following McCune (1987). (a) Numbers correspond to the following measurements: 1, HDL, head length; 2, HDD, head depth; 3, BL, body length; 4, DPTH, body depth; 5, SL, standard length; 6, PDL, pre-dorsal length; 7, PAL, pre-anal length; 8, DFPT, dorsal–pectoral length; 9, PTAL, pectoral–anal length; 10, PTPV, pectoral–pelvic length; 11, DFAN, dorsal–anal length; 12, DFPP, dorsal–pelvic length; 13, DFCD, dorsal–caudal length; 14, AFCD, anal–caudal length; 15, TDL, total dorsal fin length; 16, TAL, total anal fin length; 17, MAXCD, maximum caudal peduncle depth; 18, MINCD, minimum caudal peduncle depth; (b), Scale counts abbreviations.

**Fig. 3.** Line drawings of examples of specimens of *L. buddhabutrensis* exemplifying preservation classes. 1, very well preserved; 2, well preserved; 3, not well preserved; 4, badly preserved. Numbers refer to field numbers. Specimens are not to the same scale.
Taphonomy (Fig. 4)

State 1: The fish lies straight on one side.
State 2: The fish lies straight on one side; the squamation shows folds in the abdominal area (probably caused by expulsion of gases during decay).
State 3: The fish is partly or totally dorsoventrally preserved.
State 4: The fish is bent or twisted.

To assess the vertical variation in preservation and taphonomy, the fossiliferous deposit was divided in three sub-layers. The upper limit of the lowest layer is defined by a lithological change, from a greenish fine and loose sandstone below to a maroon mudstone above. This change may be related to a time gap in a progressive sediment deposition, or to a heterogeneity in a single rapid depositional event. As there is no visible change in the lithology in the upper part of the fossiliferous deposit, the limit between the uppermost two layers is arbitrarily defined as situated 60 cm above the lower limit. The upper layer is also about 60 cm thick.

Tests

To test whether there is more than one statistical population, the normality Shapiro–Wilk test was used. The relationship between morphometric and meristic parameters were investigated, and an allometric analysis using a linear regression of an estimation of general body size with all variables corrected for size was performed. Body size of the fish was estimated as the square root of the sum of the square of all variables. As all observations were needed to yield this body size estimator, missing values were estimated following a regression procedure: parameters of all possible regressions were computed from the available measurements. For each individual, missing values were estimated as the mean of all possible predictions from the different regressions. These estimations were performed to obtain a body size estimator only, but were not used for the other tests. The relationships between morphology (measurements and meristic) and position within the fossiliferous deposit, and between morphology and taphonomy (body posture) were analysed using ANOVA tests; the relationships between the location of individuals within the fossiliferous deposit and meristic features, taphonomy, states of preservation, and between preservation and taphonomy were tested using $\chi^2$ tests. Tests and statistics were computed with the R language and environment (Ihaka & Gentleman 1996).

### Table 1. Mean primary measurements

| Variable | HDL | HDD | BL  | DPTH | SL  | PDL | PAL | DFPT | PTAL |
|----------|-----|-----|-----|------|-----|-----|-----|------|------|
| Average  | 12.55 | 6.8 | 29.67 | 15.4 | 40.1 | 25  | 32.6 | 18.7 | 23.87 |
| Sample size | 55   | 55  | 60  | 53   | 43  | 46  | 37  | 50   | 47   |

| Variable | PTPV | DFAN | DFPV | DFCD | AFCD | TDL | TAL | MINCD | MAXCD |
|----------|------|------|------|------|------|-----|-----|-------|-------|
| Average  | 11.85| 15.98| 13.93| 18.17| 10.44| 5   | 4.36| 6.56  | 5.65  |
| Sample size | 45   | 48   | 47   | 58   | 56   | 61  | 55  | 57    | 58    |

See Figure 2 for abbreviations.
Results

Primary measurements are available as supplementary material. Mean measurements are shown in Table 1, meristic values and sample sizes for each taphonomic class are shown in Table 2, and sample sizes for preservation and taphonomy classes in each layer are shown in Table 3.

Normality of characters

Thirteen variables are normally distributed, except five: head depth (HDD, $W = 0.9128$, $n = 55$, $p = 0.0005$); dorsal–pectoral length (DFPT, $W = 0.945$, $n = 50$, $p = 0.0195$); pectoral–anal length (PTAL, $W = 0.9512$, $n = 47$, $p = 0.0483$); dorsal–anal length (DFAN, $W = 0.9038$, $n = 48$, $p = 0.0008$); maximum caudal peduncle depth (MAXCD, $W = 0.9526$, $n = 58$, $p = 0.025$). After inspection of distribution histograms, the significance of Shapiro tests is better interpreted as the presence of a few outliers in the distribution rather than the existence of several modes. Further inspection showed that outliers are the result of taphonomical processes rather than of biological abnormality. As most variables are normally distributed, and that there is no evidence of bi- or multinormality, the preserved assemblage is interpreted as belonging to a single Gaussian population.

Morphometric measurements

All but three morphometric variables are significantly and positively correlated (Table 4), indicating that these parameters are isometrically directly related to the general body size of the fish. The three exceptions are dorsal and anal fin lengths, which are significantly negatively correlated with the distance between pectoral and pelvic fin, and the anal fin length, which shows a significant negative correlation with the distance between dorsal and pelvic fin. There is no relationship between morphometric and meristic parameters, indicating that the number of scales is not related to size and does not vary during growth, as in most actinopterygians.

Allometric growth

Significant positive allometries have been detected for the distance between dorsal and pectoral fins (DFPT; $a = 0.0007$, $F$-test = 4.19, $df = 1.49$, $p = 0.04$) and for the distance between pectoral and anal fins (PTAL; $a = 0.001$, $F$-test = 5.58, $df = 1.45$, $p = 0.02$). In contrast, dorsal fin length and anal fin length (TDL; $a = -0.0004$, $F$-test = 5.77, $df = 1.61$, $p = 0.01$, TAL;
$a = -0.0003$, $F$-test $= 5.29$, df $= 1.53$, $p = 0.02$, respectively) show negative allometries (Fig. 5).

**Morphology and position within the fossiliferous deposit**

ANOVA test shows that there is no difference in the general morphology of the fish between the three layers, suggesting that the morphology of the assemblage does not vary within the fossiliferous deposit. The $\chi^2$ test did not detect any relationship between the meristic countings and the position within one of the three fish layers.

**Taphonomy, preservation and morphology**

Taphonomy was found as a source of variation for four morphological measurements: body depth (DPTH, ANOVA: $F = 9.05$, df $= 2.51$, $p = 0.0004$), dorsal–pectoral length (DFPT, ANOVA: $F = 3.31$, df $= 2.48$, $p = 0.044$), dorsal–pelvic length (DFPV, ANOVA: $F = 6.28$, df $= 2.44$, $p = 0.003$) and anal–caudal length (AFCD, ANOVA: $F = 3.92$, df $= 3.52$, $p = 0.01$). Significant differences in preservation were observed for the anal–caudal length (AFCD, ANOVA: $F = 3.92$, df $= 3.52$, $p = 0.01$) and for the dorsal fin length (TDL, ANOVA: $F = 2.82$, df $= 3.59$, $p = 0.046$).

**Mode of preservation and taphonomy**

There is no significant relationship between the preservation and the taphonomy as defined here (body posture) ($\chi^2 = 13.81$, df $= 9$, critical value $= 16.91$, $p = 0.05$). This may indicate that the postures of the carcasses are not related to the type of preservation (i.e. a specimen lying on its flank is, on average, not better or worst preserved than a specimen lying on its back).

**Mode of preservation and location within the fossiliferous deposit**

There is no significant relationship between the position of the fish in the fossiliferous deposit and the taphonomy ($\chi^2 = 4.56$, df $= 6$, critical value $= 12.59$, $p = 0.05$), but there is a significant difference between the state of preservation and the position of the fish in the fossiliferous deposit ($\chi^2 = 14.58$, df $= 6$, critical value $= 14.44$, $p = 0.025$).

**Fish orientation**

The rose diagrams show one main direction, NNW–SSE (Fig. 6), as well as a secondary orientation, which is perpendicular to the main one (ENE–WSW), for the uppermost layer (layer 1). Hydrodynamic processes oriented the fish carcasses parallel to the current, probably head against the current, or perpendicular to the current. Consequently, the main current was possibly from SSW toward NNW. Other layers show no clear main direction.

**Discussion**

The average standard length of *L. buddhabutrensis* is 401 mm, the average head length is 125.5 mm and the average body depth is 154 mm. These values represent a rather large species, compared with other species of *Lepidotes* (*L. microrhis*: 92, 30 and 46 mm, respectively, for the holotype, Wenz 2003; *L. xinjinensis*: length of 320 mm, Su 1983; *L. wenzae*, standard length (SL) estimated at 330 mm, Brito & Gallo 2003) or *Pliodetes nigeriensis* (SL $= 220$ mm, Wenz 1999) and with most species of *Semionotus* (McCune 1986), but it is rather similar in size to *Lepidotes piayhyensis* (SL ranging from 320 to 480 mm, Gallo 2005) and to *Araripelepidoidea* (SL ranging from 170 to
450 mm, Maisey 1991), and much smaller than some species of *Lepidotes* such as *L. maximus*, which could reach 2 m in total length (Jain 1985).

The negative correlation between the dorsal and anal fin sizes with the distance between pectoral and pelvic fin is partly corroborated by allometric growth of these fins, indicating that unpaired fins grow less rapidly than body size. This result shows either that the size proportions of the unpaired fins vary during growth, or that fin size, as measured on the carcasses, was influenced by external factors, such as decay. If the latter solution is correct, it indicates that the fins of large fish were affected proportionally more than fins of the small fish, because they were proportionally more exposed to decay. The other allometric pattern observed is the proportionally longer distance between pectoral and dorsal fins and between pectoral and anal fins. This gives the larger specimens a larger belly, and may be the reason for the field observation that two morphotypes seemed to be present in the fish assemblage. Our morphometric examination shows, however, that shape variations correspond to a continuum rather than to two

### Table 4. Coefficients of correlation between continuous variables

| Variables | HDL | HDD | BL | DPTH | SL | PDL | PAL | DFPT | PTAL |
|-----------|-----|-----|----|------|----|-----|-----|------|------|
| HDL       | 1.000 | 0.615* | 0.606* | 0.538* | 0.643* | 0.635* | 0.768* | 0.630* | 0.577* |
| HDD       | 0.615 | 1.000 | 0.189‡ | 0.544* | 0.299† | 0.250† | 0.499* | 0.333* | 0.175‡ |
| BL        | 0.606 | 0.189 | 1.000 | 0.324* | 0.872* | 0.745* | 0.883* | 0.613* | 0.814* |
| DPTH      | 0.538 | 0.544 | 0.324 | 1.000 | 0.283† | 0.349* | 0.419* | 0.609* | 0.327* |
| SL        | 0.643 | 0.299 | 0.872 | 0.283 | 1.000 | 0.755* | 0.783* | 0.649* | 0.645* |
| PDL       | 0.635 | 0.250 | 0.745 | 0.349 | 0.755 | 1.000 | 0.658* | 0.805* | 0.527* |
| PAL       | 0.768 | 0.499 | 0.883 | 0.419 | 0.783 | 0.658 | 1.000 | 0.580* | 0.915* |
| DFPT      | 0.630 | 0.333 | 0.613 | 0.609 | 0.649 | 0.805 | 0.580 | 1.000 | 0.636* |
| PTAL      | 0.577 | 0.175 | 0.814 | 0.327 | 0.645 | 0.527 | 0.915 | 0.636 | 1.000 |
| PTPV      | 0.285 | 0.164 | 0.673 | 0.287 | 0.586 | 0.413 | 0.681 | 0.468 | 0.671 |
| DFAN      | 0.627 | 0.408 | 0.402 | 0.599 | 0.407 | 0.190 | 0.442 | 0.448 | 0.457 |
| DFPV      | 0.644 | 0.361 | 0.444 | 0.968 | 0.477 | 0.513 | 0.463 | 0.715 | 0.364 |
| DFCD      | 0.391 | 0.337 | 0.655 | 0.225 | 0.589 | 0.360 | 0.551 | 0.378 | 0.588 |
| AFCD      | 0.299 | 0.255 | 0.342 | 0.290 | 0.284 | 0.564 | 0.227 | 0.565 | 0.192 |
| TDL       | 0.245 | 0.012 | 0.324 | 0.044 | 0.347 | 0.216 | 0.313 | 0.023 | 0.107 |
| DAL       | 0.288 | 0.333 | 0.136 | 0.110 | 0.212 | 0.181 | 0.182 | 0.180 | 0.179 |
| MINCD     | 0.604 | 0.366 | 0.343 | 0.698 | 0.481 | 0.561 | 0.447 | 0.706 | 0.304 |
| MAXCD     | 0.606 | 0.460 | 0.321 | 0.587 | 0.471 | 0.548 | 0.442 | 0.583 | 0.312 |

*Very highly significant (0 < *p* < 0.001).
†Highly significant (0.001 < *p* < 0.01).
‡Significant (0.01 < *p* < 0.05).
§Nearly significant (0.05 < *p* < 0.1).
See Figure 2 for abbreviations.
distinct morphotypes. The preserved assemblages belong to a single Gaussian population, although five parameters (HDD, DFPT, PTAL, DFAN, MAXCD) are not normally distributed. We suggest that the non-normal distributions are caused by inclusion of outliers that underwent strong taphonomic deformations. The morphology and taphonomy of the fish carcasses do not vary within the fossiliferous deposit, in contrast to the state of preservation, which varies between the fossiliferous layers. This observation might support the hypothesis that fish carcasses dried in the open air before burial by showing that fish from the lowermost layer were less affected by taphonomic decay. This hypothesis has been previously suggested on the basis of scale disarticulation, which is more reminiscent of desiccation of the body after death than rapid embedding in sediment (Cavin et al. 2004). Supporting this hypothesis is the fact that very few specimens from the lowermost layer are poorly preserved (5.6% of state 4), whereas this percentage is higher in layers 1 and 2 (16.7% and 40.6%, respectively), although the proportion of very well preserved specimens does not show the same pattern (35.7%, 15.6% and 16.7% from top, middle and bottom layers, respectively). This contradictory pattern shows either that the hypothesis is wrong (specimens from the bottom of the fossiliferous deposit are not better preserved that specimens from the top, which were supposedly more exposed to atmospheric factors causing decay before fossilization) or that the method we used is biased. The latter interpretation is possible as two strong biases are present: (1) the layers were arbitrarily defined and do not correspond to distinct events in terms of sedimentology; (2) mechanical preparation of specimens was not fully random because more specimens from the upper layer have already been prepared than specimens from the lower layers because they were the first ones to be removed from the site (42, 32 and 18 individuals, respectively) and because a choice was made to prepare the more informative specimens first. We suggest that similar analyses should be made in the future when the sample will be larger (ideally when all fishes have been prepared).
to remove the sampling bias. Another planned study (U.D.) is to assess the variability of the microstructural ornamentation of the ganoin layer at the surface of the scales, to check if the ornamentation is the same in different parts of the body of a single fish and between individuals of different sizes and states of preservation. The fact that all specimens belong to a single Gaussian population will make easier this next step of the study of the *L. buddhabutrensis* assemblage of Phu Nam Jun. The absence of relationships between preservation and taphonomy indicates that the mode of decay of the fish is not dependent on the body postures.

A weak current might explain the orientation of fish in the layers. However, the current is clearly present in the uppermost layer only (Fig. 6). It is possible that the fish have been reoriented after death subsequent to a flooding event, or to a weak current toward the centre of the drying pond where the last water remained. Another explanation is an abrupt incoming of mud that would explain the sandy layer at the base of the deposit as well as the preferred orientation of the carcasses at the top of the assemblage. Such a big mud flow, embedding several hundreds of fish individuals at the same time, might indicate strongly contrasted dry and rainy seasons. We cannot exclude, however, that the possible preferable orientation is an artefact related to the small sample sizes.

**Conclusion**

Statistical studies of morphometric and meristic features show that the prepared specimens of *Lepidotes buddhabutrensis* from Phu Nam Jun belong to a single Gaussian population rather than two as suggested by field observations of Cavin *et al.* (2004). The morphometric variables indicated that the general body size growth of fish is isometric, except for negative allometries detected on unpaired fin lengths and positive allometries detected for the distance from pectoral to dorsal and anal fins. Differences in the state of preservation show that variations in morphology are probably due to the mode of preservation. However, there is no difference between the morphology and the taphonomy of the fish carcasses within the fossiliferous deposit. A current is clearly present in the uppermost layer only.

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